The Dissertation Committee for Katherine Hilary Bannar-Martin Certifies that this is the approved version of the following dissertation:

Scale and Process: Primate and Non-Primate Mammal Community Composition and Diversity in Madagascar

Committee:

Rebecca J. Lewis, Supervisor

Mathew A. Leibold

Denné N. Reed

Anthony Di Fiore

Mariah E. Hopkins

Scale and Process: Primate and Non-Primate Mammal Community Composition and Diversity in Madagascar

by

Katherine Hilary Bannar-Martin, B.Sc., M.Sc.

Dissertation

Presented to the Faculty of the Graduate School of

The University of Texas at Austin

in Partial Fulfillment

of the Requirements

for the Degree of

Doctor of Philosophy

The University of Texas at Austin

May 2015

Dedication

For my parents, Hilary and Mark.

This would not be without you. Thank you for every sacrifice.

Acknowledgements

I have gotten a lot of results! I know several thousand things that won't work.

- *Thomas A. Edison*

It is a tough proposition to acknowledge and thank all the people that have contributed to this labour of love, time, and brainpower.

I would like to thank my advisor, Rebecca Lewis, who I met in 2006 in Ranomafana National Park, Madagascar, for sharing her love of lemurs, fieldwork, Madagascar and Anthropology with me. She has constantly reminded me to see the bigger picture, to be relevant, and to communicate effectively. Thank you to my committee: Rebecca Lewis, Mathew Leibold, Denné Reed, Anthony Di Fiore and Mariah Hopkins. I thank them for saying yes, for reading, for thinking and critiquing. I am honoured to have had them all contribute to this piece of work and honoured to have shared a room with them discussing ideas. I have been continually challenged and continually rewarded by the caliber of excellence that exists within my committee and at the University of Texas. A special thanks to Mathew Leibold for providing me with a home in the Biology department and the privilege to discuss ecological theory with his fantastic lab group.

My eternal thanks are also due to my incredible crew of peers. Kim Valenta made my first year in Austin epic, and persuaded me that Canadians in Texas are always charming. Kelsey Ellis, Addison Kemp, and Lina Valencia Rodriquez have been wonderful friends and provided compelling discussions that ran the gamut of physical anthropology, ecology, academic life, alcohol, knitting, and a lot of et cetera. Andrew Barr, Carrie Veilleuz, Amber Heard-Booth, and Rick Smith were fountains of sage advice. Thank you also to Laura Abondano, Jaime Mata-Miguez, Gabrielle Russo, Brett Nachman, Angel Zeininger for sharing the journey.

My thanks are also due to the wonderful Anthropology department at the University of Texas. Liza Shapiro's ability to question ideas until they were distilled to their simplest form was always appreciated. Chris Kirk's attention to detail and engaging teaching style have made me a better teacher. Also thank you to Billy O'Leary, Chris McNett, Adriana Dingman, and Rolee Rios, who saved my 'academic' life on several occasions, especially when I decided to finish my dissertation from Canada.

Thank you to all the people who helped along the way. Patricia Wright, Steig Johnson, and Summer Arrigo-Nelson provided data from Ranomafana National Park. Steve Goodman generously answered my emails and mailed me a pile of books, a.k.a. invaluable documents on Madagascar's fauna that supplemented my data. Charlene Nielsen provided invaluable GIS and python advice. Jesse Sinclair was my savvy [R] coding guide. Thank you also to Mishka Jada King for help with data entry. Jason Kamilar, Lydia Beaudrot and Kaye Reed, and two anonymous reviewers provided valuable comments on chapter 2.

Finally, none of this would have been possible without the support and love of my family and friends at home. My eternal gratitude is owed to my parents for instilling in me a desire for knowledge, the strength to ask questions, and the tenacity to find answers. My mother's strength, generosity and fearlessness were an inspiration and an honour to have witnessed. My father's patience has been a pillar; his quiet advice and work ethic encourage me daily to keep going. Sophie, and Emma, my incredibly talented, beautiful and wise sisters, consistently reminded me of which way is up. Thank you to my Grandma, Helen Cooper, and my godmother, Di Jones, who made my first journey to Madagascar possible. Thank you to Jenny Linton, Lindsay Horlor and Pia Nagpal for their friendship and unwavering support.

My final thanks go to the love of my life, Neil McCallum. He was the voice of realism, hope and love that got me through the last go of it.

This research was supported by a NSERC Postgraduate Doctoral Scholarship, an Explorer's Club Research Grant, an AAUW Doctoral Scholarship, and a Rhonda L. Andrews Memorial Award.

Scale and Process: Primate and Non-Primate Mammal Community Composition and Diversity in Madagascar

Katherine Hilary Bannar-Martin, Ph.D.

The University of Texas at Austin, 2015

Supervisor: Rebecca J. Lewis

The study of community assembly, or the processes that shape the occurrence of species in an ecological community, is a fundamental area of inquiry in ecology. Patterns in community composition and diversity are attributed to the combined operation of deterministic (e.g., environmental sorting), stochastic (e.g., dispersal limitation), and biogeographic (e.g., dispersal barriers) processes. Environmental sorting results in communities composed of species that are ecologically adapted to their environment. Dispersal limitation results in communities shaped by the dispersal distance between sites. Biogeographic dispersal barriers prevent species dispersal between sites, and community membership is dependent upon site isolation. Community assembly is also dependent upon diversity type (taxonomic, functional, or phylogenetic) and spatial scale.

I investigated the processes shaping the diversity of primate and nonvolant mammal communities using taxonomic, functional and phylogenetic diversity measures and a spatially explicit modelling approach. I described mammal diversity patterns at ecoregional, regional, and inter-regional scales within and across Madagascar and Australia. I tested the relationship of mammal community diversity to environmental, spatial, and biogeographic variables, indicating deterministic, stochastic, and

biogeographic processes, in Madagascar and Australia. First, I found that arboreal mammal communities in Madagascar were more dispersal-limited than terrestrial mammal communities. Second, a combination of environmental sorting and dispersal limitation best explained primate taxonomic and functional diversity. Third, I tested for convergent diversity and assembly patterns in Madagascar and Australia, due to similar biogeographic and evolutionary histories, and found non-convergent patterns. Overall, biogeographic dispersal barriers were weak predictors of mammal diversity in Madagascar and Australia. Phylogenetic and functional diversity measures were weakly correlated, and phylogenetic diversity provided models with weak explanatory power. Environmental and spatial variables indicating the combined operation of environmental sorting and dispersal limitation variably shaped the taxonomic and functional diversity of mammal communities in Madagascar and Australia. Mammal community diversity was regionally specific, shaped by the unique historical and landscape components of each region, including ecoregional effects and the extinction of sympatric species. Macroscale studies of diversity should carefully investigate the influence of spatial scale and regional factors that can result in varied assembly patterns and unique ecological communities, such as those present for the nonvolant mammals of Madagascar and Australia.

Table of Contents

List of Tables

List of Figures

Chapter 1: Introduction – Mammal Community Assembly

INTRODUCTION

Understanding the processes that shape patterns in community composition and diversity continues to be an important area of inquiry in community ecology. In contrast to species-specific studies, community ecology strives to elucidate the relationships (1) among species, and (2) between species and their environment. The study of interspecies interactions explains how species can successfully co-exist, co-occur, and compete with each other. However, species do so on an environmental stage composed of different climates, geographies, evolutionary histories, and stochastic forces. Extensive searches have been made to identify the existence of patterns of nonrandomness within communities and the assembly "rules" that govern these patterns (e.g., Clements 1916; Connor and Simberloff 1979; Diamond 1975; Gleason 1926; Hubbell 2001; Keddy 1992; Fox and Brown 1993; Hubbell 2001; Kraft et al. 2007; Leibold et al. 2004; MacArthur and Levins 1967; Mac Arthur and Wilson 1963; Pacala and Tilman 1994; Watkins and Wilson 2003; Weiher et al. 2011; Weiher and Keddy 1995, 1999; Wilson and Whittaker 1995). The study of community assembly attempts to explain how species come together or stay together in intact ecological communities (Weiher and Keddy 2001) and tries to explain these patterns through the action of assembly processes.

The study of community assembly is directed toward understanding the rules by which species come together to form communities (Diamond 1975; Keddy 1992), and can allow for the study of such rules in a clade's evolutionary past (Chase and Myers 2011) and potentially use such rules to describe future diversity distributions (Chase and Leibold 2003). Since the study of community assembly is concerned with understanding how environmental variables and dispersal limitation, as examples, shape diversity

distributions, it provides useful information for understanding how diversity distributions have been and will be shaped by environmental change, for example how certain traits related to dispersal limitation shape the ability of species to succeed in a fragmented landscape. Much debate over the past decade in community assembly has been concerned with identifying which processes predominantly shape community composition across a variety of taxa (e.g., Adler 2004; Bell 2001; Chave 2004; Dornelas et al. 2006; Condit et al. 2002; Gilbert and Lechowicz 2004; Harpole and Tilman 2006; Hubbell 2001; McGill 2003; McGill et al. 2006; Tuomisto et al. 2003; Volkov et al. 2003; Wootton 2005;). Three sets of processes have been hypothesized to play a role in shaping primate and mammal communities.

The first, deterministic processes (niche differentiation, environmental sorting, and competitive exclusion) are driven by niche-based processes (Chase and Leibold 2003; Chase and Myers 2011; Gause 1934; Hutchinson 1957) wherein communities are composed of nonrandom sets of species that have species-specific niches. One example of a deterministic process is environmental sorting, where communities are composed of species adapted to the environment within which they live and resemble communities inhabiting similar environments (Chase and Leibold 2003; Leibold et al. 2004; Tilman and Pacala 1993). In which case environmental variables, describing the abiotic environment can be used to detect ecological similarity and the presence of environmental sorting (Chase 2003, 2007; Kamilar 2009). The second, stochastic processes (neutral theory, dispersal limitation by distance, environmental stochasticity, demographic stochasticity), by contrast, do not require species-specific niches, and instead community composition is the result of random colonization and extinction dynamics (Bell 2001; Chase and Myers 2011; Chave 2004; Hubbell 2001; MacArthur

and Wilson 1967; Tokeshi 1999). Stochastic processes give rise to patterns of species diversity, relative abundance and composition that are indistinguishable from random chance (Chase and Myers 2011), and can exist in multiple forms (Hubbel 2001; MacArthur and Wilson 1967; Tokeshi 1999). Dispersal limitation is one measure of stochastic processes, and is the limited dispersal of individuals through their isolation from other communities by distance, limited range expansion, limited movement and unsuccessful establishment in new areas (Condit et al. 2002; Chave and Leigh 2002; Gilbert and Lechowicz 2004; Hubbell 2005; Jone et al. 2006). Communities shaped by dispersal limitation more closely resemble communities that are geographically close together than communities that are geographically distant from each other. In this case, spatial variables, describing the distance between sites can be used to detect the presence of dispersal limitation by distance (Condit et al. 2002; Chave and Leigh 2002).

Although deterministic and stochastic processes have been the subject of most debate (Adler 2004; Bell 2001; Chave 2004; Condit et al. 2002; Dornelas et al. 2006; Gilbert and Lechowicz 2004; Harpole and Tilman 2006; Hubbell 2001; McGill 2003; McGill et al. 2006; Tuomisto et al. 2003; Volkov et al. 2003; Wootton 2005), I argue that biogeographic processes are a third set of processes that should be considered separately and integratively with deterministic and stochastic processes (detailed below and in Chapter 2). Although biogeographic processes are not often tested in conjunction with deterministic and stochastic processes, they have also been suggested to shape community composition by influencing regional species pools from which local communities are composed (Ricklefs and Schluter 1993; Wiens and Donoghue 2004). These biogeographic processes include colonization, historical dispersal events, and biogeographic dispersal barriers (Simpson 1953; Tokeshi 1999; Vences et al. 2009).

Biogeographic dispersal barriers affect the spread and survival of species, by physically preventing the dispersal of species into other areas (Tokeshi 1999; Vences et al. 2009). They differ from stochastic dispersal limitation because it is a physical property of the habitat, such as a river or mountain range, not distance that prevents dispersal. Species are therefore found in areas they are not physically prevented from dispersing. Biogeographic variables, describing the effect of biogeographic barriers on dispersal (e.g., Chan et al. 2011; Fischer et al. 2011; Vignieri 2005) can then be used to detect the contribution of biogeographic barriers to community assembly.

While deterministic, stochastic, and biogeographic processes have been studied independently, recognition now exists that assembly processes work as part of an integrated continuum (Adler et al. 2007; Chase and Myers 2011; Gravel et al. 2006; Leibold and McPeek 2006; McGill et al. 2006; Figure 1.1). Deterministic, stochastic, and biogeographic processes have all been identified and supported as individual determinants of the distribution of primate and mammal species and communities (e.g., Beaudrot and Marshall 2011; Ganzhorn et al. 1997; Ganzhorn 1998; Gavilanez and Stevens 2013; Kamilar 2009; Muldoon and Goodman 2010). Spatial scale also influences the assembly processes that contribute to observed diversity distributions (e.g., Dray et al. 2012; Mouchet et al. 2010; Pavoine and Bonsall 2011). Few studies exist however testing the contribution of multiple processes to the assembly of primate communities. In this dissertation, I investigate the relative contribution of deterministic, stochastic and biogeographic processes to the assembly of nonvolant mammal communities, with an emphasis on the assembly of primate communities in Madagascar. I achieve this goal by explicitly considering spatial scale in shaping assembly scenarios, and by investigating the contribution of diversity type to the identification of assembly processes. This

introductory chapter provides a condensed overview of theoretical developments in the study of mammal community assembly and describes the objectives, analytical approach and structure of this dissertation.

MAMMAL COMMUNITY ASSEMBLY

Community assembly rules can be broadly defined as any filter imposed on a regional species pool that acts to determine local community structure and species composition (Keddy 1992), and thus, determines community patterns in space and time (Figure 1.2). However, the majority of community assembly research has been conducted on plants (Adler et al. 2007; Chu et al. 2007; Duarte 2011; Stokes and Archer 2010) and invertebrates (Cadotte 2007; Rominger et al. 2009). As such, development and testing of principles of community assembly have been mostly limited to the study of sessile organisms. Consequently, there is a relative dearth of studies on vertebrate community assembly, particularly that of mammals. However, this research bias is changing, and more studies concerning mammals (e.g., Ernest et al. 2008; Esselstyn et al. 2011; Fox 1987; Kelt 1995; Lomolino 2000; Mendoza et al. 2004; Morris 2005; Raia 2010; Riddle 2006; Svenning et al. 2011), including primates (e.g., Beaudrot and Marshall 2011; Ganzhorn 1997; Gavilanez and Stevens 2013; Muldoon and Goodman 2010), are being published.

Mammals play diverse roles in ecological communities as predators, prey, seed dispersers, and habitat modifiers (e.g., Bourlière 1985; Fleagle et al. 1999; Herrera 2002; Kamilar and Beaudrot 2013; Reed and Bidner 2004), and are thus important components of food webs and interspecific interactions, including competition. Furthermore, mammal orders include wide ranges of variation in morphological and behavioural traits, generating varied patterns in distribution and assembly. Such traits include short and long

lifespan, small to large body size, varied dispersal distances by species and throughout life stages, varied geographic ranges, slow or fast reproductive history, sophisticated social behaviour, and varied cognitive abilities (e.g., Dayan and Simberloff 1994; Hayes and Jenkins 1997; Nunn and Barton 2001; Wright 1999). Mammals occupy a variety of niches and have complex patterns of space and habitat use, which might not comply with hypotheses derived from models based on plants or non-vertebrate fauna. While plants are sessile and fixed in place, with only their seeds dispersing across spatial scales, mammals disperse or travel throughout their lives and interpret spatial landscapes very differently, minimizing or altering the notion of a "local" scale (Weiher et al. 2011). Such fundamental differences can result in differences in community assembly and the relative importance of regional and local processes (e.g., Jenkins 2007; Weiher et al. 2011). Despite the relative paucity of mammal community assembly research, mammals are a relatively well-studied group, with extensive datasets on their traits, distributions, and evolutionary histories (e.g., Bininda-Emonds et al. 2007; Jones et al. 2009; Kamilar and Beaudrot 2013; Nowak 1999).

Primates, in particular, are key components of tropical forest vertebrate biomass (e.g., Chapman et al. 2010; Hawes and Peres 2013). Consequently, understanding the factors that shape primate communities can help identify the factors that shape tropical mammal distributions. Primate species distributions are well studied, and they provide an excellent reference point for comparative studies in community ecology, macroecology, and conservation biology (Kamilar and Beaudrot 2013). However, primate species do not exist in ecological communities in isolation, they interact with other vertebrate species (e.g., Beaudrot et al. 2013b, 2014; Kamilar et al. 2014; cf. Karpanty 2006; Marshall et al. 2009; Schreier et al. 2009) and a comprehensive understanding of the factors shaping

primate mammal community diversity requires an understanding of their sympatric competitors, i.e. nonprimate mammal species.

The study of mammal community assembly departs from non-vertebrate models in three important and interacting ways: (1) the contribution of stochastic processes (measured as dispersal limitation) may be decreased because mammals have the ability to move over the landscape, (2) the contribution of biogeographic processes (measured as effective dispersal around barriers) may be greater because they can physically prevent dispersal over the landscape, and (3) the contribution of deterministic processes may be more complex because the variety and range of trait values and phylogenetic histories across scales present in mammal communities might generate novel inter- and intraspecies relationships. Furthermore, the larger spatial scales incorporated in a mammal species' interpretation of a landscape is more likely to result in patterns of environmental sorting (Weiher et al. 2011).

COMMUNITY ASSEMBLY PROCESSES

Natural communities are shaped by deterministic, stochastic, and biogeographic processes (Cadotte 2007), which interact to shape community composition and diversity (Figure 1.1). Viewing deterministic, stochastic, and biogeographic processes as part of a continuum allows researchers to consider which process contributes the most (or least) information about a given diversity pattern (Alonso et al. 2006; Zilio and Condit 2007). An integrative model of process bridges the conceptual gap between deterministic, stochastic, and biogeographic theories, and highlights the theoretical weakness in approaches to community ecology that start with the assumption that structure in communities arises from niche differentiation among species (Hubbell 2006). The relative roles of deterministic, stochastic, and biogeographic processes in determining

patterns of diversity have practical implications for predicting community responses to anthropogenic change (Chase and Leibold 2003) and for distinguishing the extent to which competitive interactions have shaped extinct and extant communities and evolution (Chase and Myers 2011). Without an integrated model of process, discerning the extent to which species traits, species interactions, and environmental conditions contribute to deterministic community structure relative to stochastic forces, and to what extent biogeographic processes relate to the structure of ecological communities is not possible (cf. Wiens and Donaghue 2004). The development of a more comprehensive understanding of mammal community composition and diversity will show how assembly processes interact where observations deviate from solely deterministic, stochastic, or biogeographic predictions.

Deterministic processes

Deterministic processes involve nonrandom, niche-based mechanisms (Chase and Leibold 2003; Chase and Myers 2011). For example, traits that allow individuals or a species to gather resources, evade enemies, and influence life history are deterministic (Grinnel 1917; Hutchinson 1957). Deterministic processes predominate if species' abilities to establish in a locality are more strongly determined by their traits than by stochastic colonization and extinction dynamics (Chase and Leibold 2003). Nonrandom patterns in species distribution can also result from environmental sorting (species sorting, ecological sorting). Spatial heterogeneity in environmental factors that affect fitness, such as resources and abiotic conditions, result in species associations with particular habitat types (Reynolds et al. 2007; Tilman and Pacala 1993). Habitat quality and dispersal can result in large differences in the demography and outcomes of species' interactions at the local scale, and can cause species to associate along environmental

gradients. Patterns of diversity are the result of spatial niche separation instead of dispersal limitation by distance (a stochastic process; Chase and Leibold 2003; Huston 1994; Leibold et al. 2004; Tilman and Pacala 1993).

Deterministic processes can be described by parameters that describe a species' resource use and traits and a site's ecological character (Chase and Myers 2011). For example, the ecological similarity of community habitats is a useful proxy measure for species sorting and environmental filtering (Chase 2003, 2007; Kamilar 2009) because ecologically similar sites are likely to have similar community composition (Chase and Myers 2011). Consequently, deterministically assembled communities are expected to have more predictable community composition, with low site-to-site variation in composition and low β-diversity in communities with similar environmental conditions (Chase 2010; Dornelas et al. 2006; Tuomisto et al. 2003).

Studies of mammal community composition have largely been concerned with deterministic processes (e.g., Amori and Luiselli 2011; Badgley and Fox 2000; Cardillo and Meijaard 2010; Fox 1987; Fox and Kirkland 1992; Ganzhorn 1997; McGill et al. 2005; Smith and Ganzhorn 1996), or limited by data collected over a short period of time (Morris 2005). Long-term studies of mammals (e.g., Fryxell et al. 1998; Marcstrom et al. 1990; Oksanen and Oksanen 1992) provide support for deterministic processes among species, but other assembly mechanisms remain largely unexplored (but see Beaudrot and Marshall 2011; Fox 1987; Morris 2005).

In primates, deterministic processes are also supported with factors such as body size, activity pattern, diet, canopy use, tolerance to poor food quality during times of scarcity (Cannon and Leighton 1994; Marshall et al. 2009; Schreier et al. 2009, reviewed in: Kamilar and Beaudrot 2013; Reed and Bidner 2004) having been described as axes of

niche differentiation. Interspecific competition between primate and nonprimate species can also be important in determining species distributions (e.g., Beaudrot et al. 2013b, 2014; Kamilar et al. 2014; cf. Karpanty 2006; Marshall et al. 2009; Schreier et al. 2009). Spatial and ecological factors that determine habitat specialization might have an influence on primate community composition (Kamilar 2009; Peres and Janson 1999), including the area of tropical forest (Reed and Fleagle 1995), mean annual rainfall (Reed and Fleagle 1995), habitat heterogeneity (Bourlière 1985), fruit production (Stevenson 2001), latitudinal gradients (Stevenson 2001), plant species richness (Stevenson 2001), extent of closed forest cover (Cowlishaw 1999), soil fertility (Emmons 1984; Oates et al. 1990), and environmental gradients (Muldoon and Goodman 2010). For example, in Madagascar variation in leaf protein and fruit availability were correlated with primate species richness (e.g., Hanya and Aiba 2010; Hanya et al. 2011; Simmen et al. 2012). At the community level, environmental variables were relatively weak predictors of primate community structure in Africa, Asia and the Neotropics (Beaudrot and Marshall 2011; Gavlilanez and Stevens 2012; Kamilar 2009), but species turnover in Madagascar was best explained by environmental sorting (Beaudrot and Marshall 2011).

Stochastic processes

Stochastic process describes any ecological process that gives rise to a pattern of species diversity, relative abundance, or composition that is indistinguishable from a pattern that would arise from random chance (Chase and Myers 2011). Stochasticity can be demographic, environmental, or can refer to colonization or extinction (Hubbell 2001; MacArthur and Wilson 1967; Tokeshi 1999), therefore, models of community composition and assembly must be carefully parsed to recognize a stochastic element (Tokeshi 1999). Recently, the unified neutral theory of biodiversity (Hubbell 2001,

hereafter neutral theory) has challenged the role of deterministic processes in explaining biodiversity patterns. Neutral theory suggests that species rich communities can be created by considering only stochastic processes of birth, death, colonization, speciation, and extinction (Bell 2001; Chave 2004; Hubbell 2001). The neutral ecological drift of species abundances predominantly controls species assemblages (Bell 2001; Hubbell 2001).

Ecological drift in neutral theory leads to dispersal-assembled communities, with the structure of these communities resulting from stochastic colonization and extinction processes, rather than species traits (Hubbel 2001). In this view, abiotic and biotic variables are inconsequential in the establishment and persistence of a species and colonization is dependent upon dispersal and survival within available areas. Distance is thought to strongly influence species dispersal, and therefore, community composition, because community similarity between sites decrease with increasing distance between sites (Chave and Leigh 2002; Condit et al. 2002; Gilbert and Lechowicz 2004; Hubbell 2005; Jones et al. 2006). Stochastic events involving species demography and dispersal are the foundation of diversity patterns (Hérault 2007; Hubbell 2001, 2005; Jones et al. 2006). Because neutral processes are driven by random events, and all individuals are competitively identical, species abundances either increase or decrease purely by chance (McGill et al. 2006).

Stochastically assembled communities, through dispersal limitation by distance, are expected to have considerable site-to-site variation in their community composition among otherwise similar environments (Chave and Leigh 2002; Condit et al. 2002). Stochastically assembled communities can be distinguished from biogeographically assembled communities where dispersal is not constrained by biogeographic dispersal

barriers and is instead the result of distance limited dispersal (cf. Wright 1943), limited range expansion, limited movement, or unsuccessful establishment in new areas (cf. Wiens 2011). The relative importance of ecological drift, leading to dispersal-assembled communities, is greater when dispersal is low, when niche-selection is weak, and/or when priority effects are strong (e.g., early colonization can establish a population, which provides a competitive advantage over future colonists; Chase 2007; Connell and Slatyer 1977; Shulman et al. 1983; Sutherland 1974). When stochastic processes predominate, communities with high site-to-site variation in species composition can emerge with high species turnover even when environmental conditions among sites are similar (Chase et al. 2009). Low compositional similarity among communities that are identical in environmental conditions, or high compositional similarity among communities that are geographically close to each other, implies a large role for dispersal limitation by distance (Chase 2003, 2007; Chase et al. 2005; Chave and Leigh 2002).

However, stochastic variation in community composition and diversity may also be attributed to a failure to take into account the importance of historical events and unmeasured environmental variables (or unexplained variation) (Legendre and Legendre 1998). Unexplained variation can be an artefact of the methods being used (Økland 1999), due to measurement error (Clark et al. 2003), or due to a lack of model fit (Legendre and Legendre 1998; Økland 1999).

A few studies have examined stochastic processes as a potential determinant of mammal community composition and diversity, with mixed results. For example, Morris (2005) found that stochastic processes of species invasion and persistence shape community membership in small mammals, in addition to the action of deterministic processes. Similarly, stochastic processes in the form of dispersal limitation by distance

are stronger determinants of primate global primate community structure than environmental sorting in Africa, South America, and Borneo (Beaudrot and Marshall 2011) and neotropical primate populations (Gavilanez and Stevens 2013). Geographic distance between sites has also been suggested as important determinates of lemur communities (Ganzhorn 1998; Kamilar 2009) and Guyanan primate communities (Lehman 2006), with increased distances leading to decreased similarity in composition. El Niño Southern Oscillations may also determine local patterns of primate species co-occurrence, suggesting a role of environmental stochasticity (Lawes and Eeley 2008).

Biogeographic Processes

Biogeographic phenomena, including dispersal barriers, affect the survival and spread of species populations (Tokeshi 1999). Riverine barriers, riverine basins, and mountain ranges can act as biogeographic filters, preventing species from occupying all ecologically ideal habitats (Vences et al. 2009; *sensu* faunal filter: Simpson 1953). Large rivers can form semi-permanent geographical barriers that some species are unable to cross, with the strength of the barrier decreasing toward their narrow headwaters (Vences et al. 2009). Though biogeographic processes are viewed by some as being stochastic (e.g., Chase and Myers 2011; Hubbell 2001), thinking of them as separate from stochastic dispersal limitation by distance is useful in the case where species colonize new habitats and evolve *in situ* within a biogeographic framework, as has happened with mammals in Madagascar (Yoder et al. 2003) and Australia (Fooden 1972).

Although biogeographic processes are rarely explicitly tested alongside deterministic and stochastic processes, their inclusion in any study of community assembly is necessary to understand patterns of community composition (Chase and Myers 2011; Condit et al. 2002; Holt 1993; Kraft et al. 2011; Nekola and White 1999;

Qian et al. 2005; Ricklefs 1987; Ricklefs and Schluter 1993; Tuomisto et al. 2003; Whittaker 2006). Ricklefs (2006) made several recommendations for the inclusion of biogeographic processes in the study of assembly: (1) characterize species distributions over the gradients within which they interact; (2) examine patterns of distribution within a phylogenetic context; (3) characterize diversification rates across gradients; (4) incorporate phylogeographic data to detect speciation; and (5) incorporate extinction patterns into descriptions of diversity patterns.

Biogeographic dispersal barriers also compound spatial distances between sites and thus may interfere with deterministic or stochastic processes being detected in a study of community assembly. Biogeographically assembled communities are similar only within bounded areas. Separation of biogeographic dispersal barriers from stochastic dispersal limitation (which may instead describe migration limits) allows communities bounded by biogeographic dispersal barriers to first be influenced by biogeographic process, and then by deterministic processes. This distinction would not be detectable if all forms of dispersal limitation (biogeographic and stochastic) were grouped under the same process. The stochastic process of dispersal limitation by distance is often measured as the Euclidean distance between sites (e.g., Beaudrot and Marshall 2011; Thompson and Townsend 2006; Tuomisto et al. 2003), by contrast, the action of biogeographic processes can be measured as the effective distance between sites (e.g., Chan et al. 2011; Fischer et al. 2011; Vignieri 2005). Biogeographic features that modify the ability to disperse over a landscape are explicitly considered when measuring the distance between sites, so the effective distance is a better approximation of how far away sites actually are from each other (Bannar-Martin 2014).

A discussion of biogeographic processes remains incomplete without a discussion of phylogeography. Phylogeographic research attempts to infer the origin of biogeographic structuring of genetic variation within and among closely related species across landscapes by using genealogical relationships among DNA sequences (Avise 2000; Emerson et al. 2011). Phylogeographic methods have proliferated in recent years and now provide novel ways of investigating community assembly processes through evolutionary time (Emerson et al. 2011; Hickerson et al. 2010). However, very few tests of phylogeographic methods on community assembly have been performed (Emerson et al. 2011). In a detailed study of the historical biogeography of Amazonian tree species and potential role of biogeographic processes in driving community-level patterns of species turnover Dexter et al. (2012) found that historical/biogeographic processes have limited species' distributions and directly influence present-day patterns of community assembly, even at small spatial scales.

Biogeographic processes have also received support in studies of mammal communities (Brown 1971, 1978; Harcourt and Wood 2012; Lomolino and Davis 1997; Rickart 2001). For example, water is an effective biogeographic barrier for terrestrial mammals (Harcourt and Wood 2012), including primates (Ayres and Clutton-Brock 1992; Goodman and Ganzhorn 2004a; Martin 1972; Meijaard and Groves 2006). African rivers restrict the distribution of many primate species (Harcourt and Wood 2012). In Madagascar, rivers have been found to be biogeographic barriers for a variety of species, including primates (*Avahi occidentalis, Eulemur rufus, Microcebus berthae*, *Phaner parienti,* and *Propithecus verereauxi*) and other mammals (*Echinops telfairi, Galida elegans occidentalis*, *Geogale aurita, Hypogeomys antimena, Mungotictis decemlineata*, and *Oryzorictes talpoides*) (Andriaholinirina et al. 2006). In addition, river basins can act

as biotic refugia in Madagascar and become centers of species endemism due to isolation from other areas (Wilmé et al. 2006; Wilmé and Callmander 2006). Mountain ranges and elevation changes can act as biogeographic barriers to mammal distributions (e.g., Cortes-Ortiz et al. 2003; Ron 2000; Simpson 1964). For example, Andreone et al. (2009) suggest that the position of Marojejy, a montane site in northern Madagascar, may contribute to differences in species composition in neighbouring forest sites (Raxworthy et al. 1998). Using phylogeographic methods, Stone and Cook (2000) showed that biogeographic features (e.g., refugia, ice sheets) shaped the colonization routes of black bear species and community assembly in Alaska.

DIVERSITY AND COMMUNITY ASSEMBLY

Central to a discussion of community assembly is a notion of community composition, richness, or diversity, whereby similarity between two communities can be assessed. Recent research on community assembly has shifted away from solely measuring species diversity to also using trait- and/or phylogenetic-based measures (Cavender-Bares et al. 2009; Hardy and Senterre 2007; Pavoine et al. 2010; Silvertown et al. 2006; Webb et al. 2002). Different measures of taxonomic (taxonomic identity of species), functional (the functional role species are playing in an ecosystem) and phylogenetic diversity (amount of evolutionary history each species contributes) have been proposed (Magurran and McGill 2011; Pavoine and Bonsall 2011). However, taxonomic, functional, and phylogenetic diversity patterns often differ (Pavoine and Bonsall 2011; Figure 1.3), generating various community assembly interpretations (e.g., Kraft and Ackerly 2010; Meynard et al. 2011; Pavoine and Bonsall 2011). In Figure 1.3, four hypothetical communities demonstrate that high taxonomic diversity does not necessarily equate with high functional or phylogenetic diversity, resulting in varied

diversity patterns for the same community. Furthermore, different measures depend on the type of individual-level data available, occurrence (presence/absence) data or abundance data. The majority of assemblage lists for mammals are comprised of occurrence data (Weiher et al. 2011). Consequently, I focus on diversity metrics that can use occurrence data.

Taxonomic Diversity

Taxonomic diversity, particularly species richness (McIntosh 1967) and beta diversity (Gering and Crist 2002), are the most commonly used diversity measures in the study of community assembly because species are the fundamental units of ecological research. Discussions of species diversity require taxonomic identification of each member of a community, whether it is at a species, genus, or family level. While several definitions or species concepts exist and are the subject of much debate (reviewed in De Quieroz 2007), I will not discuss the merits of different notions of capturing species differences here.

The first formalized measurement of species differences between communities was with Whittaker's (1960) realization that environmental gradients occur within local communities as well as span multiple communities. Three hierarchical levels of biodiversity followed to assess compositional patterns and community assembly along environmental gradients at different spatial scales: alpha (α), beta (β), and gamma (γ) diversity. Alpha diversity quantifies the number of species at a local scale, or within a habitat. Beta diversity quantifies the amount of species turnover between habitats. Gamma diversity measures the species richness of a region (McIntosh 1967; Whittaker 1960; Whittaker et al. 2001).

Communities with high γ-diversity have histories of openness to new species with weak constraints on assembly (Weiher and Keddy 1999). However, diverse communities are also characterized by many rare species, potentially increasing the importance of demographic stochasticity over niche-based processes (e.g., Barot 2004). Consequently, where α-diversity is high, neutral assembly might predominate (Weiher et al. 2011) as has been suggested for tropical tree communities (e.g., Hubbel 2001). Alternatively, studies using measures of taxonomic β- diversity suggest that communities with high β-diversity become diverse because niche-based constraints on assembly are relatively weak (Chase et al. 2009; Chase 2007, 2010), or strong patterns of environmental sorting predominate (Chase and Leibold 2003; Leibold et al. 2004). High β-diversity could also be due to priority effects, where the order of arrivals dictates success and helps shape community diversity (Chase 2010; Connell and Slatyer 1977; Ejrnæs et al. 2006; Leibold et al. 2004; Shulman et al. 1983; Sutherland 1974). Interpretations of patterns in taxonomic diversity are complicated by the lack of a clear relationship between α and β-diversity and each may respond differently to assembly processes (Gering and Crist 2002). Furthermore, the taxonomic diversity approach is limited because it does not take into account dissimilarities among species in terms of their traits or phylogenetic history, and cannot alone describe processes involved in species coexistence and ecosystem functioning (Cianciaruso 2011). Furthermore, taxonomic-based studies are limited to the specific habitats those taxa are found, and thus cannot be easily extrapolated to understand community assembly in habitats with different taxa.

Phylogenetic Diversity

Measures of phylogenetic diversity describe the amount of evolutionary history shared among species (Faith 1992; Webb 2000, 2002). The study of community

phylogenetic diversity has provided insights regarding the roles of species interactions and biogeographic histories in community assembly (e.g., Cavender-Bares et al. 2009; Gavilanez and Stevens 2013). Furthermore, the study of phylogenetic niche conservatism, the tendency of species to retain ancestral ecological characteristics (Wiens and Graham 2005), and assembly processes has allowed for predictions regarding patterns of phylogenetic relatedness and assembly (Webb et al. 2002). Phylogenetic clustering (Figure 1.4) is hypothesized to be evidence for environmental sorting of conserved traits (Webb 2000), and overdispersion (or evenness; Figure 1.4) is evidence for limiting similarity due to competition between closely related species (phylogenetically and functionally; Kraft et al. 2007; Violle et al. 2012) or environmental sorting of traits that evolved convergently (Cavender-Bares et al. 2004; Helmus et al. 2007a, 2007b). Phylogenies are assumed to represent unmeasured or complex traits better than a limited number of measured traits (Cavender-Bares et al. 2009; Helmus et al. 2007a, 2007b; Mouquet et al. 2012). Furthermore, phylogenetic relatedness can be used as a proxy measure for functional diversity, and can therefore be useful if trait data are not available and if the observed traits are phylogenetically conserved (Kraft et al. 2007; Prinzing et al. 2001). However, the use of phylogenetic diversity as a measure of trait variation has been criticized (e.g., Bernard-Verdier et al. 2013; Pavoine and Bonsall 2011; Pavoine et al. 2013), and has mixed support (e.g., Flynn et al. 2011; Meynard et al. 2011; Safi et al. 2011) because the assumption that phylogenetically related species are also functionally related does not always hold (e.g., Kamilar and Cooper 2013; Swenson 2011).

Overall, mammal communities trend toward phylogenetic overdispersion, where co-occurring species are distantly related (e.g., Cardillo et al. 2008; Cardillo 2011;

Cooper et al. 2008; Kamilar and Guidi 2010; Kamilar et al. 2014; Figure 1.4), however some exceptions apply. New World monkey assemblages and North American ground squirrel assemblages are phylogenetically overdispersed, but Australasian possums are not (Cooper et al. 2008). Ungulate, primate (not including Malagasy species), and fruit bat island assemblages are typically phylogenetically overdispersed, but additional biogeographic factors influence the amount of overdispersion (Cardillo et al. 2008). Malagasy and mainland African primate species are phylogenetically randomly structured with tendencies toward overdispersion or clustering depending on the clade (Kamilar and Guidi 2010; Kamilar et al. 2014). Carnivore communities show nonrandom clustered or overdispersed patterns of phylogenetic diversity, depending on ecoregion and spatial scale (Cardillo 2011). Rodent communities show a strong negative relationship between environmental heterogeneity and phylogenetic distance (Stevens et al. 2012). Communities were phylogenetically overdispersed in areas of low heterogeneity and clustered with increasing heterogeneity, possibly due to areas of higher resource availability that favour large numbers of species (Stevens et al. 2012). A recent study of neotropical primate taxonomic and phylogenetic community assembly also found that spatial variables explained the majority of the variation in two measures of phylogenetic diversity (mean pair-wise phylogenetic distance and mean nearest taxon phylogenetic distance) (Gavilanez and Stevens 2013). A large proportion of variation was also explained by joint spatial-environmental-evolutionary variables, however, suggesting that environmental and biogeographic effects also structure Neotropical primate diversity at broad spatial scales (Gavilanez and Stevens 2013).

Despite the applicability of phylogenetic measures to studying community assembly in extinct communities, few examples exist. PlioPleistocene large mammal

communities of western Eurasia were found to have changed significantly around 1 Ma, when communities were filled with closely related species from carnivore and herbivore clades (Raia 2010). In primates, a study of extinct subfossil primate communities in Madagascar showed patterns of phylogenetic overdispersion, similar to extant lemurs (Razafindratsima et al. 2013).

Functional Diversity

The trait based approach to measuring diversity, hereafter functional diversity, has been proposed as a way to reconcile assembly hypotheses within ecology (Lavorel and Garnier 2002; McGill et al. 2006). A functional trait is any morphological, physiological, or phenological trait that affects an organism's growth, reproduction, or survival and, ultimately, fitness (McGill et al. 2006; Violle et al. 2007). Community ecologists have been able to predict community composition and ecosystem functioning from quantitative information that describes the functional differences between individuals of different species as well as between individuals of the same species (Lavorel and Garnier 2002). Increasingly, community ecologists have sought to generate functional trait information for all species in their study systems as a means to test how both biotic and abiotic factors influence diversity patterns across space (Diaz and Cabido 1997; Weiher and Keddy 1995; Weiher et al. 1999; McGill et al. 2006). However, this approach is still predominantly used only with plants.

The study of functional diversity and community assembly suggests that trait variation among co-occurring species is shaped by environmental sorting and competition (Diamond 1975; Keddy 1992; Weiher and Keddy 1995; Weiher et al. 1998), with environmental sorting shaping communities across different ecosystems (e.g., Cornwell and Ackerly 2009; Kraft et al. 2008; Swenson and Enquist 2009). Although functional

traits reflect adaptations to different environments, environmental sorting acts upon whole individuals and therefore a suite of multiple traits (Grime 2002; Westoby et al. 2002). Therefore, interspecific correlations between traits reflect the action of natural selection that facilitate the existence of certain trait combinations (Westoby et al. 2002).

The study of functional diversity is recommended (e.g., Ackerly and Cornwell 2007; McGill et al. 2006; Pavoine and Bonsall 2011; Weiher and Keddy 1995) because assembly rules based on species traits have many advantages over species-based rules (Weiher and Keddy 1995). One particular advantage is that it is traits, not taxon names, which are the fundamental units of species sorting (McGill et al. 2006; Weiher and Keddy 1995). Many functional diversity metrics have been developed to describe multiple aspects of trait distribution (reviewed in Petchey and Gaston 2006; Mouchet et al. 2010; Schleuter et al. 2010). Within a community, functional diversity may include the kind, range, and relative abundance of trait values (Diaz and Cabido 2001; Mason et al. 2005). The majority of published metrics, however, quantify functional richness and are highly correlated (Mouchet et al. 2010). For the study of community assembly, measures of functional diversity are ideally continuous, account for multiple functional traits and species abundances, and measure multiple facets of diversity (Mason et al. 2005; Mouchet et al. 2010; Petchey and Gaston 2006; Villéger et al. 2008). Several complementary measures fit these criteria and can be used with occurrence data (Figure 1.5), including functional richness (FRic), functional divergence (FDiv), functional dispersion (FDis), and Rao's Quadratic Entropy (RaoQ). These measures have been found to accurately differentiate community assembly processes (*sensu* Laliberté and Legendre 2010; Mason et al. 2013; Mouchet et al. 2010). These measures provide community-level metrics that describe aspects of richness (FRic),

divergence (FDiv), and dispersion (FDis and RaoQ) in the distribution of traits and their values in trait space that are present in a community.

Functional diversity as a community-level metric has not been investigated often in mammal fauna, although patterning in functional groups have been investigated (e.g., Fox and Brown 1993; Fox and Fox 2000; Ganzhorn et al. 1997; Muldoon and Goodman 2010). New World bat functional diversity showed patterns in functional richness with latitudinal gradients, which was unrelated to patterns of variation in species richness (Stevens et al. 2003). Community responses to resource variation were thought to have contributed to the differences observed in functional diversity at local versus regional scales (Stevens et al. 2003). In a more recent study, global bird and mammal assemblages showed differences in trait diversity at local versus the regional pools; this was attributed to environmental sorting (Belmaker and Jetz 2013). For mammals specifically, communities with low functional differences have been shown to contain fewer local species implying that competition constrained local mammal species richness (Belmaker and Jetz 2013).

COMMUNITY ASSEMBLY ACROSS SPATIAL SCALES

The composition and diversity of communities is structured by processes that operate at a variety of scales (Dunning et al. 1992; Leibold et al. 2004; Peterson and Parker 1998; Wiens 1989), and attributes of assemblages are highly dependent on the scale at which they are examined (Angermeier and Winston 1998; Caley and Schluter 1997; Elith and Leathwick 2009; Mackey and Lindenmayer 2001; Ricklefs 1987; Whittaker 1972; Willis and Whittaker 2002). Spatial scale is therefore a covarying element in any study of community assembly.

Through space, communities reflect effects such as differences in habitat, differences in dispersal ability, and at large scales, differences in geographical ranges and biological regions (Morris 2005). Consequently, spatial scale is known to affect the relative importance of different processes (deterministic, stochastic, and biogeographic) and the strength of the signal detected for those processes (Figure 1.2; Keil et al. 2012; Leibold et al. 2004; Rahel et al. 1984). The dominant drivers of community assembly may change with spatial scale (Cavender-Bares et al. 2006; Emerson and Gillespie 2008; Swenson et al. 2006). At the local scale, niche processes, competition and direct interactions operate (cf. Harrisson and Cornell 2008). Consequently, deterministic processes are most likely to dominate at local or small spatial scales (Figure 1.2). Conversely, stochastic processes are expected to dominate at regional spatial scales (Figure 1.2), where patterns of dispersal limitation by distance and neutral assembly are detectable, especially for motile species. Biogeographic processes are expected to prevail at interregional scales because biogeographic barriers are large-scale entities and the number of biogeographic barriers increases with larger spatial scales, resulting in more apparent patterns of biogeographic filtering at large spatial scales than may be evident at small spatial scales (Figure 1.2; cf. Lomolino and Davis 1997). At the largest spatial scales, species distributions are determined by biogeographic processes (i.e., geographic patterns of speciation, extinction, and migration; Figure 1.2).

The relative influence of local and regional processes on species richness varies among assemblages, but no community is likely to be structured by processes operating solely at local or regional scales (He et al. 2005; Loreau 2000). However, most empirical studies of the determinants of community structure have been conducted at the local scale, probably because of the logistic constraints associated with larger spatial scales and

the pervasiveness of competition and niche theory in models of the determinants of species richness in a community (Williams et al. 2002). Nevertheless, geographic distances shape patterns of turnover at large regional scales, suggesting that stochastic processes are operating (e.g., Baselga 2008; Keil et al. 2012; Qian et al. 2005; Qian and Ricklefs 2007; Svenning et al. 2011).

The spatial scale of study affects measures of taxonomic diversity (Loreau 2000). Movements of individuals between spatial scales act as a homogenizing force, leading to a reduction in β-diversity while increasing α-diversity because immigration continues to maintain local coexistence (Loreau and Mouquet 1999). Alpha-diversity is expected to decrease at fine spatial scales because the number of individuals is reduced and strong direct interactions dominate the community, thereby increasing β-diversity (Loreau 2000). Conversely, the importance of α-diversity to overall regional diversity is more important at larger spatial scales because local interactions are less important or undetectable (Huston 1999; Loreau 2000). Decreases in β-diversity within small spatial scales also occur because, as sampling grain increases, the variability of the mean environmental conditions decreases (Levin 1992; Mac Nally et al. 2004), which has been shown in birds (Lennon et al. 2001; Keil et al. 2012; Mac Nally et al. 2004), mammals (Arita and Rodríguez 2002), plants, butterflies, amphibians, and reptiles (Keil et al. 2012). Finally, environmental correlates of β-diversity are scale dependent, because both the distributions of individual species (Elith and Leathwick 2009; Mackey and Lindenmayer 2001) and species richness (Willis and Whittaker 2002) have different environmental correlates at different scales.

Spatial scale can influence the functional diversity evident in each community. For example, traits associated with species' abilities to obtain resources in a particular

environment operate at the local scale (Morin and Lechowicz 2008), whereas the traits that are related to dispersal might reveal patterns of functional diversity that are structured on larger scales. Consequently, the choice of traits can influence the sensitivity of functional diversity measures to various spatial scales (e.g., Ackerly and Cornwell 2007).

Scale has been shown to be important in a variety of clades, including terrestrial vertebrates (Caley and Schluter 1997, Robinson et al. 2000), fish (Angermeier and Winston 1998; Poizat and Pont 1996), insects (Lawton et al. 1993; Pearson and Juliano 1993), coral reefs (Karlson and Hurd 1993), and vascular plants (Kohn and Walsh 1994; Palmer and White 1994), generating spatial patterns in diversity. For example, at regional scales, phylogenetic turnover is shaped by allopatric speciation or adaptive speciation with environmental gradients, resulting in strongly disjunct distributions or strongly divergent spatial niches between closely related species (Graham et al. 2009). At larger (continental) scales, by contrast, phylogenetic turnover is dominated by limited spatial niche evolution and/or limited dispersal (Eiserhardt et al. 2013).

DISSERTATION OBJECTIVES

This dissertation attempts to clarify the processes shaping the composition and diversity of primate and mammal communities using a spatially explicit and integrative modelling method. I describe patterns of nonvolant mammal community diversity and assembly at three different spatial scales: (1) an ecoregional scale, (2) a regional scale (entire island of Madagascar), and (3) an interregional scale (Madagascar and Australia), and address the following questions:

1. Are arboreal and terrestrial species separately shaped by environmental sorting, dispersal limitation, and biogeographic barriers?

2. Are taxonomic, functional, and phylogenetic diversity measures of community richness differentially explained by deterministic, stochastic, and biogeographic processes?
3. Can patterns in process be generalized across ecoregions, and do they show patterns of convergence across regions of similar biogeographic and evolutionary histories?

DISSERTATION STUDY AREAS

Madagascar

Madagascar is an ideal region for investigating patterns of community diversity and assembly (Vences et al. 2009). It is home to diverse endemic fauna that are species-rich and relatively well known (Goodman and Benstead 2005). The extant nonvolant terrestrial mammals of Madagascar include 4 orders (Afrosoricida, Carnivora, Primates and Rodentia), 8 families, 38 genera and 207 species (IUCN 2014). Of these, primates are represented by 5 families, 15 genera, and 99 endemic species (Mittermeier et al. 2008). Lemurs arrived in Madagascar 50–80 Ma (Horvath et al. 2008; Poux et al. 2005; Yoder and Yang 2004). Lemuriforme divergence postdates the separation of Madagascar from other landmasses, and the first ancestral lemurs are hypothesized to have arrived on Madagascar via oceanic dispersal (Ali and Huber 2010). Their arrival was followed by at least two prominent episodes of lineage diversification (Horvath et al. 2008; Yoder and Yang 2004) coinciding with environmental change in Madagascar. The first divergence was between *Daubentonia* and the common ancestor of all remaining lemurs. The second divergence occurred between the end of the Eocene and through the Oligocene (23.8–40 Mya). During this period rainforests began emerging in Madagascar (Wells 2003; Yoder and Yang 2004). In addition, discrete colonization events of carnivores, tenrecs, and

rodents in Madagascar also occurred (Poux et al. 2005). Additional shifts in vegetation have occurred since the Late Pleistocene with an island-wide transition toward more open vegetation (Burney 1987a, 1987b; Burney 1993; Burney et al. 1997, Burney et al. 2004, Gasse and Van Campo 1998; Matsumoto and Burney 1994; Virah-Sawmy et al. 2009). The combination of environmental change, arrival of novel competitors and the already diversifying lineage of lemurs resulted in rapid and widespread lineage diversification and adaptive radiation within the lemuriformes (Horvath et al. 2008) and nonvolant mammals of Madagascar (cf. Muldoon and Goodman 2010).

Today, Madagascar is described by regionally pronounced and locally steep environmental gradients, patterns of microendemism across taxa and numerous evolutionary radiations, making it an ideal location within which to examine the roles of deterministic, stochastic and biogeographic processes (Vences et al. 2009). The island is differentiated into ecogeographic areas or ecoregions based on floristic and rainfall patterns (e.g. Burgess et al. 2004; Olson et al. 2001). Temperatures are highest on the coast and decline inland (Burgess et al. 2004; Goodman and Benstead 2003). Precipitation and precipitation seasonality increase from the north to the south and from the east to the west, and these differences tend to coincide with elevational differences, and a mountainous ridge running the midline of Madagascar from the north to south. The east of Madagascar, characterized by humid forests, receives the most precipitation from trade winds and little to no dry season. The west of Madagascar characterized by the spiny thickets, and dry deciduous forest is comparatively extremely dry with high precipitation seasonality and environmental stochasticity due to seasonal cyclones (reviewed in Crowley 2010; Muldoon and Goodman 2010).

The widespread diversification of mammals in Madagascar across varied environments has resulted in unique suites of traits that distinguish both lemurs from anthropoid primates and endemic nonprimate mammals from congeners in other regions. In lemurs these traits include female dominance in many species, lack of notable sexual dimorphism, strict seasonal breeding in most species, and cathemerality (Wright 1999). Various hypotheses have been proposed to explain the uniqueness of Malagasy primates, including the energy frugality hypothesis where low basal metabolic rate, small group size, torpor and seasonal breeding are thought to be adaptations to energy conservation, and female dominance, folivory, territoriality and cathemerality are adaptations to resource scarcity (Wright 1999). The evolutionary disequilibrium hypothesis has also been proposed to explain the presence of cathemerality and diurnality in lemurs due to the recent extinctions of large diurnal predators (van Schaik and Kappeler 1996), however this hypothesis has been countered (Griffin et al. 2012; Kirk 2004, 2006). The nonprimate mammals of Madagascar are also described by the presence of species with unusual life history patterns, activity periods and dietary preferences. For example the Tenrecidae range widely in body mass from 3g to over 2000g, and one species (*Tenrec ecaudatus*) can have up to 32 neonates in a litter, the largest of any mammal (Dewar and Richard 2007). The Tenrecidae of Madagascar also use torpor as an energy conservation mechanism, similar to the Cheirogaleid primates (e.g., Lovegrove and Génin 2008). Like primates, the carnivores of Madagascar have strict seasonal breeding and give birth only once a year, differentiating them from Carnivora in other regions (Dewar and Richard 2007). While most of the nonvolant mammal species of Madagascar are nocturnal, cathemerality exists in one carnivore species (*Cryptoprocta ferox;* Gerber 2012) and the *Brachyuromys* rodent genera (Nowak 1999). The wide range of traits present in

Madagascar's nonvolant mammal species (cf. Muldoon and Goodman 2010) suggests varied adaptations to environmental gradients that provide interesting tests of deterministic processes at the community-level.

Recent studies of primates (Beaudrot and Marshall 2011; Gavilanez and Stevens 2013) that tested deterministic and stochastic assembly processes showed stochastic processes are important components of primate communities in mainland Africa, Asia, and the neotropics. Madagascar, however, did not fit global assembly patterns and was better explained by deterministic processes. This difference from other primate regions leads to questions of why this difference may exist, and whether the nonprimate mammal communities of Madagascar are also uniquely assembled. Muldoon and Goodman (2010) in a study of nonvolant mammal distributions in Madagascar found that community composition was strongly determined by ecological or environmental characteristics. However, the effects of biogeographic barriers or dispersal limitation were not examined.

Australia – a Useful Comparison

In addition to understanding how unique Madagascar is on its own, it is more appropriate to compare Madagascar's faunal patterns to a landmass with a similar biogeographic and evolutionary history, than to other primate regions. Australia provides an interesting and useful comparative region to Madagascar for three main reasons. First, the processes shaping the composition of communities are more easily investigated on an island than in a larger land mass because islands are discrete and bounded (Whittaker 1998), and both Madagascar and Australia are bounded in space. While Madagascar is classified geographically as an island (cf. de Wit 2003), and Australia is classified as a continent or an island continent (cf. Cawood and Korsch 2008), they are both

characterized by bounded borders within which their mammal diversity can be described and quantified.

Second, Madagascar and Australia share similar biogeographic histories, and yet contain both similarly and differently structured habitats. Both regions have long histories of independent radiation in similar biophysical environments and shared ancestral Gondwanaland biota (Ezcurra and Agnolin 2012; Jokat et al. 2003; Reeves and de Wit 2000). The modern distribution patterns of arboreal mammals in Australia and Madagascar suggest that the first arboreal mammals may have had to compete with similar species on both continents (Smith and Ganzhorn 1996). Additionally, Madagascar's physical environment is similar to that of northeastern Australia. Both Madagascar and Australia contain tropical evergreen rainforests in the east characterized by high rainfall, and both regions have seasonally dry and deciduous rainforest in the northwest. These rainforests are similar in structure and flora, potentially due to a common ancestry and land connection via India in the late Cretaceous Period (Smith and Ganzhorn 1996). However, the semi-arid environments of both regions support endemic and structurally unique vegetation (Smith and Ganzhorn 1996).

Third, both Madagascar and Australia are host to large numbers of endemic mammalian species that have been the result of isolated and disparate evolution events. Both regions' extant, nonvolant mammal populations are the result of independent and discrete colonization events (cf. Archer et al. 1999; Jansa et al. 1999; Kay and Hoekstra 2008; Olson and Goodman 2003; Weyeneth et al. 2011; Woodburne and Case 1996; Yoder et al. 1996, 2003) with long periods of isolation, which have resulted in unique assemblages of species (Fooden 1972; Williams et al. 1996; Woodburne and Case 1996; Yoder et al. 2003). Consequently, Australia and Madagascar have vertebrate assemblages

that are the most phylogenetically distinct globally (Holt et al. 2013, cf. Kreft and Jetz 2013). T

Fourth, convergence in niche structure in the arboreal lemurs of Madagascar and the possums and gliders of Australia has been previously hypothesized and demonstrated in their dietary niches (Smith and Ganzhorn 1996). For example, *Daubentonia madagascariensis* in Madagascar and *Dactylopsila* spp. in Australia both have specialized third fingers for extracting grubs and fill the woodpecker niche in their respective habitats (Ganzhorn et al. 2014). Both regions also have specialized arboreal mammalian folivores, represented by the Indriids, bamboo lemurs, woolly lemurs and lepilemurs in Madagascar (Goodman and Benstead. 2003), and koalas, tree kangaroos, and possums in Australia (Nowak 2005). Consequently the biogeographic history, evolutionary history, and adaptive trait structures that are present in both Madagascar and Australia provide an interesting comparison for testing convergent diversity patterns and assembly at the community-level in these two speciose regions.

ANALYTICAL APPROACH

This dissertation employs a unifying analytical approach for revealing the combined influence of environmental, spatial, and biogeographic effects on the assembly of mammal communities (Figure 1.6). The action of deterministic, stochastic, and biogeographic processes in the assembly of ecological communities cannot be measured directly. Instead, proxies have to be used to indicate the role of assembly processes in shaping community diversity. Environmental sorting, one type of deterministic process, leads to species being found in environments to which they are best adapted, consequently environment variables describing various environmental attributes are useful proxies for measuring the action of environmental sorting (Chase 2003, 2007;

Chase and Myers 2011). Stochastic processes, of which one type is dispersal limitation by distance, shapes communities by limiting dispersal over large distances. Consequently, the Euclidean (straight-line) distance between sites is a useful proxy measure for detecting the contribution of dispersal limitation shaping community diversity (Chase 2003, 2007; Chase et al. 2005; Chave and Leigh 2002). Finally, biogeographic processes can be indicated by measures of relative site isolation due to the prevention of dispersal by biogeographic dispersal barriers (Ricklefs 1987; Vences et al. 2009). Consequently, I present a measure of site isolation based on the effective dispersal distance between sites taking into account eh cost of traveling around or over biogeographic dispersal barriers (chapter 2).

In this dissertation, I test the relationship between environmental variables and community diversity to detect environmental sorting, and consequently that deterministic processes are operating; I refer to these as environmental effects. Secondly, I use the spectral decomposition of the Euclidean distance between sites, detailed below, to indicate the action of dispersal limitation by distance and therefore stochastic processes shaping diversity; I refer to these as spatial effects. Finally, I use the biogeographic effective distance ratio, introduced in chapter 2, to indicate the operation of biogeographic dispersal barriers and therefore biogeographic processes in shaping community diversity; I refer to these as biogeographic effects (Figure 1.6).

An understanding of relationships among explanatory variables and their relative influence on diversity is particularly relevant to a discussion of community assembly (Adler et al. 2007; Chase et al. 2009; Gravel et al. 2006; Leibold and McPeek 2006). Many methods for detecting community assembly processes have been suggested, including checkerboard distributions, Mantel tests, spectral decomposition, variation

decomposition, maximum entropy models, and structural equation modelling (Diamond 1975; Dray et al. 2012; Grace et al. 2010; Shipley et al. 2006; Table 1.1). However, only a few of those methods are spatially explicit and capable of modelling species-environment relationships or modelling multiple spatial scales (see Dray et al. 2012 for a detailed discussion on most methods).

Spectral decomposition is used to describe the spatial relationships among geographic locations to produce a set of multiscale spatial explanatory variables (Dray et al. 2006). The principal coordinates of neighbour matrices (PCNM) approach is one type of spectral decomposition used to model and identify the spatial variables describing Euclidean distances between sites in a dataset. PCNM is a particular case of Moran's eigenvector maps, which uses Moran's I (an index of spatial autocorrelation) and a spatial weighting matrix defined by Euclidean distances between study sites (Dray et al. 2006). Consequently, the PCNM approach is spatially explicit (Table 1.1) and accounts for the effects of spatial autocorrelation. Most ecological data are subject to the effects of spatial autocorrelation, which is ubiquitous in geographically based data (Diniz-Filho et al. 2003; Dormann et al. 2007), and increases standard errors and inflates type I errors (Lichstein et al. 2002). In endogenous processes, the spatial pattern is generated by factors that are inherent properties of the variable itself (Fortin and Dale 2005), such as reproduction, dispersal, speciation, extinction, or geographical range extension (Diniz-Filho et al. 2003; Legendre 1993). Conversely, spatial autocorrelation induced by exogenous processes is independent of the variable of interest (Fortin and Dale 2005), and includes spatially structured environmental factors such as geomorphological processes, wind, energy input, or climatic constraints, which can cause species distributions to be spatially structured (Diniz-Filho et al. 2003; Legendre 1993). The

PCNM approach can be used to detect significant correlations of diversity with variables independent of spatial autocorrelation and at a variety of spatial scales (Borcard and Legendre 2002; Borcard et al. 2004). Consequently, I employ this method in this dissertation to model the spatial distances describing dispersal limitation and to identify the spatial structures influencing environmental and biogeographic variables.

PCNM analysis uses eigenfunctions of spatial connectivity matrices to create spatial predictors (PCNM variables) that can be directly included in regression models to model spatial structures at all spatial scales (Griffith and Peres-Neto 2006). The first PCNMs represent broad scale spatial structures, with successive PCNMs representing progressively smaller spatial scale effects (Borcard and Legendre 2002). Consequently, PCNMs with positive eigenvectors can be separated into various spatial scale categories to reflect the spatial grain of the study sites. Furthermore, PCNM eigenvectors that depict spatial scales are orthogonal and independent to avoid multicollinearity (Dray et al. 2006). PCNM tests also work well with presence/absence data and community data from multiple sites across space (Legendre et al. 2005), which makes it an appropriate method for the study of primate and mammal diversity.

Variation partitioning can then be used following a PCNM analysis to identify the components of variation in a community composition that are explained by deterministic effects, stochastic effects, and biogeographic barriers (Gilbert and Lechowicz 2004; Heino et al. 2010; Jones et al. 2008; Karst et al. 2005; Legendre et al. 2005; Lindo and Winchester 2007; Sattler et al. 2010; Smith and Lundholm 2010). Variation can be partitioned into proportions due purely to (1) environmental variables (environmental effects) which can be attributed to environmental sorting, or deterministic processes; (2) PCNMs (spatial effects) which can be attributed to dispersal limitation by distance, or

stochastic processes; and (3) biogeographic variables (biogeographic effects) which can be attributed to biogeographic processes (*sensu* Laliberté et al. 2009). Where variation is shared between PCNMS and other components of variation (environmental variables and biogeographic effective distance ratios), the component of shared variation is understood to be spatially structured. In the modelling approach used in this dissertation community diversity is always the response variable, and the environmental, spatial and biogeographic variable sets are always the explanatory variables. The explanatory variables testing the contribution of assembly processes are constant throughout the dissertation, with only the response variable, the diversity quantified, changing. Variation partitioning is then used to quantify the amount of variation attributable to the different sets of deterministic, stochastic, or biogeographic variables and estimates the relative importance of the different processes that determine community structure (e.g., Cottenie 2005; but see Smith and Lundholm 2010; Figure 1.6).

CHAPTER OVERVIEW

Chapter 2

Chapter 2 contains an analysis of the assembly processes that shape Madagascar's nonvolant mammal communities using PCNM of the spatial relationships among study sites and variation decomposition to describe and compare (i) primates to nonprimate mammals, and (ii) arboreal to terrestrial mammals to detect varying patterns of community assembly. Previous studies have suggested that primate communities are dispersal limited, except in Madagascar where environmental effects have shaped communities (Beaudrot and Marshall 2011). However, previous work did not investigate the role of biogeographic barriers. Furthermore, the relative roles of these processes are

potentially specific to taxonomic and/or functional groups due to a group's ecological preferences. The goals of this chapter are to identify to what extent environmental sorting, dispersal limitation by distance, and biogeographic barriers shape patterns of primate and nonprimate community composition, in comparison to terrestrial and arboreal mammal communities in Madagascar.

Chapter 3

Chapter 3 presents an investigation of how different measurement indices of diversity are shaped by different community assembly processes and how this might inform future studies of community assembly. Patterns in community variation are usually documented using taxonomic diversity measures, including between community beta diversity. However, communities can also be described functionally by the ecologically important traits they possess (functional diversity). Using functional and phylogenetic diversity metrics across taxonomic groups can provide insights into how environmental factors shape diversity, and may indicate the operation of different assembly processes. Functional diversity analyses are particularly relevant where phylogenetic and ecological similarity are not strongly correlated, such as for the primates of Madagascar (Kamilar and Guidi 2010; Kamilar and Muldoon 2010). Using occurrence and trait data of primate communities in Madagascar, I calculate taxonomic, functional, and phylogenetic diversity metrics for each community. I then compare the detected contribution of deterministic, stochastic, and biogeographic processes to community diversity measures using PCNM and variation partitioning.

Chapter 4

Chapter 4 provides a test of convergent assembly scenarios in two regions with similar biogeography and histories of isolated mammal evolution, Madagascar and Australia, with an investigation of similarities and differences in community assembly patterns of nonvolant and arboreal mammals in shared and nonshared ecoregion types. Taxonomic, functional, and phylogenetic diversity are compared between regions and ecoregions, and detected community assembly patterns (with PCNM and variation partitioning) for diversity type are compared between regions. Patterns and assembly of functional diversity in the arboreal mammal communities of Madagascar and Australia are expected to be similar due to previously discovered convergence in functional affinities (cf. Smith and Ganzhorn 1996).

Chapter 5

Chapter 5 provides general conclusions to the questions posed in the dissertation and suggests further directions for the study of community assembly. Such future directions include suggestions for the study of community assembly in paleocommunities, and for the prediction of community-level changes in regions with climate change and modified landscapes. I also review the merits of a multi-diversity approach to the study of community assembly, paying particular attention to the relative utility of functional and phylogenetic approaches.

Table 1.1. Overview of the major approaches to studying community assembly in ecological communities. Examples provided from studies on mammals where possible and indicated by an asterix.

Method and reference	Community Composition Data Required	Model more than one process?	Spatially Explicit? [a]	Examples
Checkerboard distributions				
Diamond 1975	Occurrence or abundance	No (measures deterministic against null)	Yes, but low power	Beaudrot et al. 2013b*; Ellis et al. 2009*; Kamilar and Ledogar 2011*; Nijman and Nekaris 2010*
Partial Canonical Ordination				
Borcard et al. (2004)	Occurrence or abundance	Yes	Yes	Carlson et al. 2010; Svenning et al. 2004
Mantel/Partial Mantel Tests				
Mantel 1967, Legendre and Troussellier 1988	Occurrence or abundance	No (measures comparative fit of each process)	No	Beaudrot and Marshall 2011*; Freestone and Inouye 2006
Distance-based Moran Eigenvector Maps and Variation Decomposition				
Borcard et al. 1992, Borcard and Legendre 1994	Occurrence or abundance	Yes	Yes	Bannar-Martin 2014*; Gavilanez and Stevens 2013*; Griffith and Peres-Neto 2006
Maximum Entropy				
Shipley et al. 2006; Shipley 2010	Abundance	Yes	Yes	Laughlin et al. 2011; Mokany and Roxburgh 2010; Shipley et al. 2011
Structural Equation Modeling/Path Analysis				
Shipley 2002, Grace 2006	Occurrence or Abundance	Yes	Yes, with a spatial latent variable; spatial weighting; or separation into spatial lag distances [b]	Anderson et al. 2011; Bannar-Martin 2013*; Lebrija-Trejos et al. 2010; Weiher et al. 2011

[a] taken from Dray et al. 2012, unless otherwise specified

[b] Folmer and Oud 2008; Lamb et al. 2014; Liu et al. 2011

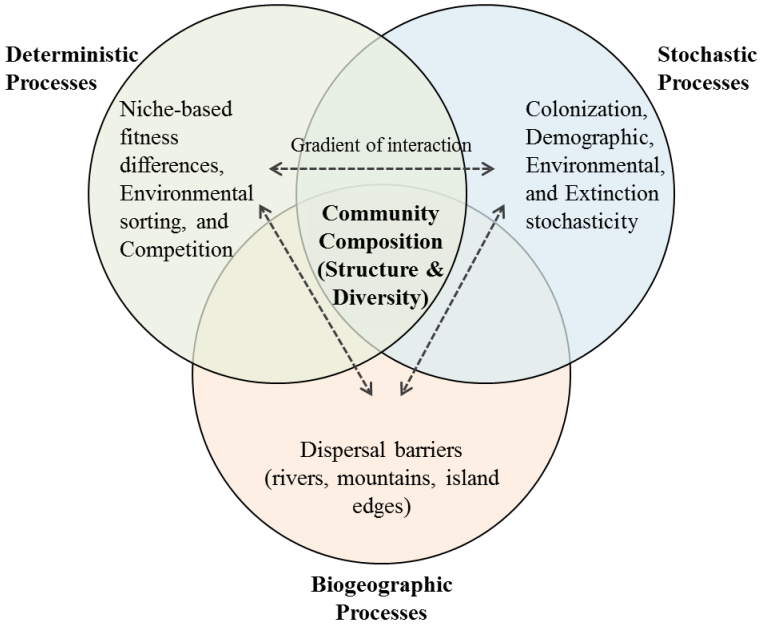


Figure 1.1. Schematic of how processes interact to shape biotic community composition and diversity.

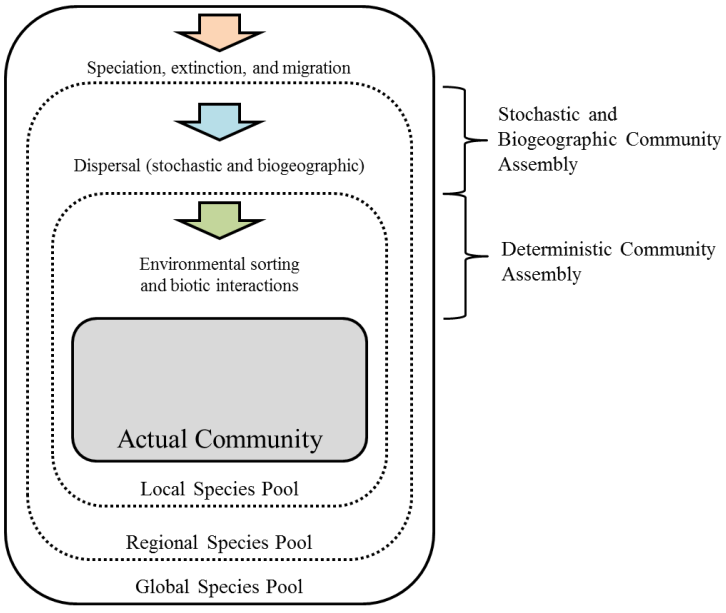


Figure 1.2. Community assembly processes and the spatial scales at which they operate (modified from Zobel 1997).

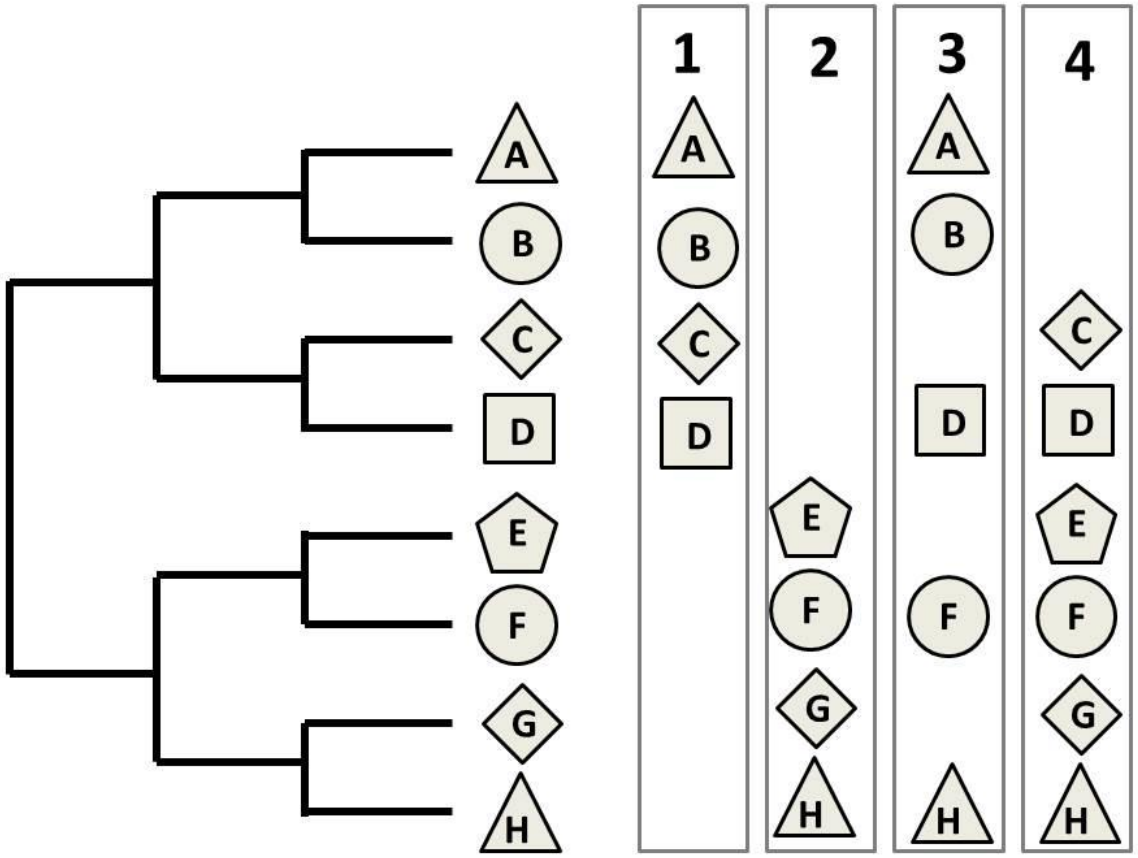


Figure 1.3. Schematic illustrating the differences between different ways of capturing community composition and diversity. Each community is indicated by a separate column numbered 1 to 4. Each letter indicates the phylogenetic affinity of each species as indicated by the cladogram on the left. Each shape indicates different functional affinities. In this example, community 1 has (i) lower species richness than communities 3 and 4, (ii) high functional diversity with 4 traits represented, and (iii) low phylogenetic diversity with only half of the cladogram represented. By comparison, community 3 has (i) higher species richness than community 1, (ii) lower functional diversity, and (iii) the highest phylogenetic diversity of all the communities.

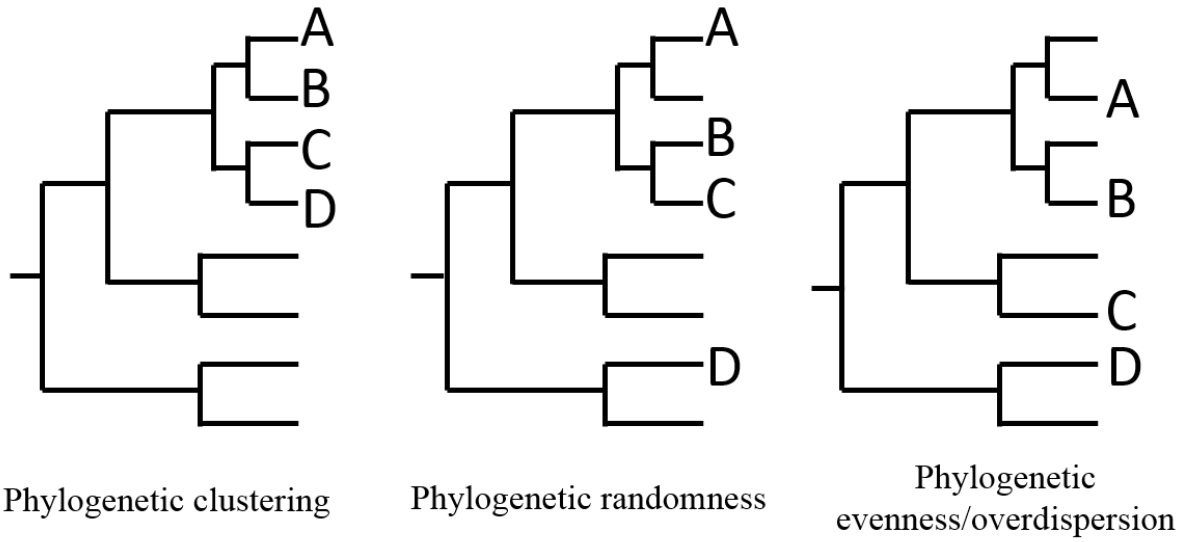


Figure 1.4. Schematic of community phylogenetic structure (adapted from Kamilar et al. 2014). The tips of the trees represent the species that make up the species pool. The letters at the end of the tips represent the species present in a hypothetical community made up of four species.

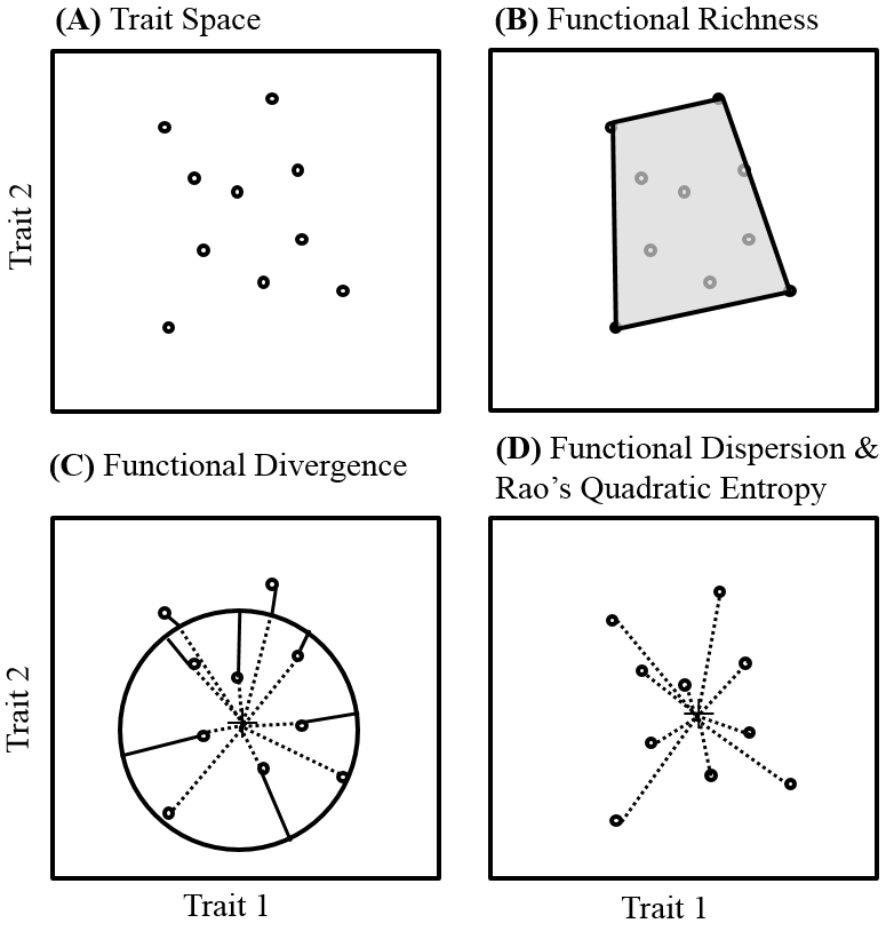


Figure 1.5. Schematic representations of functional diversity metrics used in this study. **(A)** Distribution of two hypothetical traits in trait space. **(B)** Functional richness represents the hull volume of trait space present in the community (Villéger et al. 2008). **(C)** Functional Divergence represents community variation in traits determined by the distribution of species abundances in niche space (Villéger et al. 2008). **(D)** Functional Dispersion (FDis) and Rao's Quadratic Entropy (RaoQ) are both measures of functional dispersion, and are similarly calculated, however RaoQ is the weighted variance, and FDis is the weighted mean absolute deviation of species' distances from the community trait centroid adjusting for occurrence (Laliberté and Legendre 2010). Images modified from Villéger et al. (2008), and Laliberté, and Legendre (2010).

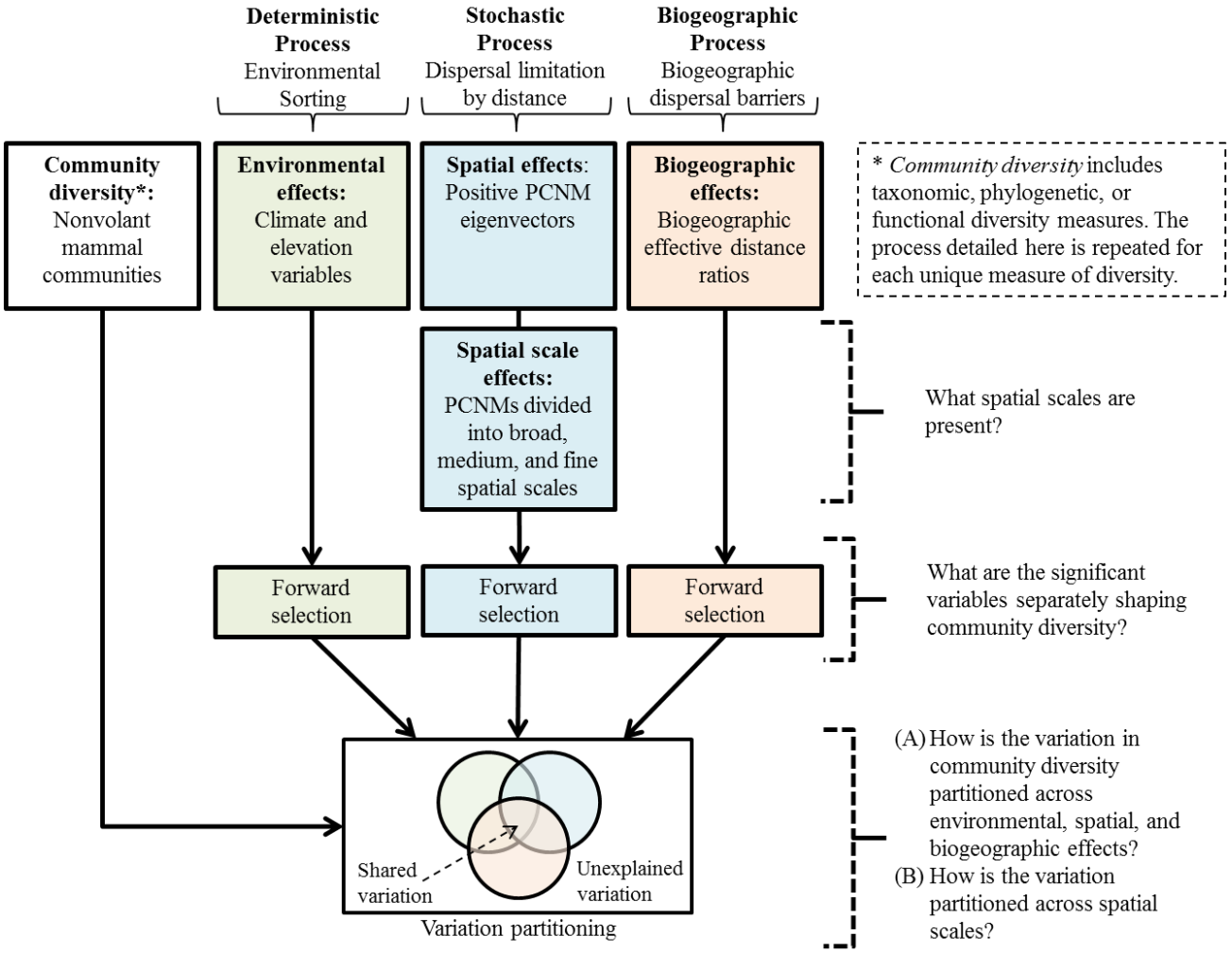


Figure 1.6. Schematic representation of methodological approach used in this dissertation. PCNM, Principal Coordinates of Neighbour Matrices.

Chapter 2: Primate and non-primate mammal community assembly - the influence of biogeographic barriers and spatial scale

INTRODUCTION

Ecological communities form through a complex interplay of community assembly processes (e.g., Chase and Myers 2011; Diamond 1975). At least three processes have been separately hypothesized to influence the formation of ecological communities, which are broadly categorized as deterministic (niche differentiation, environmental effects) (Chase and Leibold 2003; Chase and Myers 2011), stochastic (spatial effects, neutral theory, dispersal limitation by distance, mid-domain effect, environmental stochasticity, demographic stochasticity) (Colwell and Lees 2000; Hubbell 2001; Lees et al. 1999; MacArthur and Wilson 1967; Tokeshi 1999), and biogeographic processes (historical process, evolutionary process, biogeographic barriers) (Simpson 1953; Tokeshi 1999; Vences et al. 2009). Most of this research examined organisms other than primates (reviewed in Cottenie 2005; cf. Beaudrot and Marshall 2011; Beaudrot et al. 2014; Gavilanez and Stevens 2013; Kamilar 2009). The extent to which each of these processes contributes to the formation of ecological communities, however, varies by clade and geographic region (e.g., Condit et al. 2002; Qian and Ricklefs 2012). Although processes operate in a non-mutually exclusive framework (e.g., Chase and Myers 2011; Gravel et al. 2006; Leibold and McPeek 2006), identifying and comparing components and contributions of each process to community assembly will further understanding of environmental and spatial influences on community structure (e.g., Chase and Myers 2011; Gravel et al. 2006; Leibold and McPeek 2006).

Previous studies of deterministic and stochastic processes have been predominantly focused on the roles of environmental effects and dispersal limitation in

shaping community assembly (e.g., Beaudrot and Marshall 2011; Lindo and Winchester 2009; Morris 2005). The role that biogeographic dispersal barriers, or vicariance events, have played in shaping community assembly has gone largely unexplored (cf. Gavlilanez and Stevens 2013), despite the importance of historical biogeographic barriers in community assembly (e.g., Condit et al. 2002; Ricklefs 1987; Tuomisto et al. 2003). Studies have shown that biogeographic barriers can shape patterns of mammal diversity (e.g., Brown 1978; Harcourt and Wood 2012; Lomolino and Davis 1997) and patterns of endemism in Madagascar (Pastorini et al. 2003; Pearson and Raxworthy 2009; Wilmé et al. 2006). For example, rivers serve as boundaries or refugia for some nonvolant mammals in Madagascar (Ganzhorn et al. 2006; Goodman and Ganzhorn 2004a; Pastorini et al. 2003; Pearson and Raxworthy 2009; Wilmé et al. 2006). In addition, mountain ranges and elevation changes can act as biogeographic barriers to mammal distributions (e.g., Cortes-Ortiz et al. 2003; Goodman and Ganzhorn 2004b). Patterns of extant community composition can also be the result of speciation generating different species assemblages. In Madagascar these include speciation events shaped by ecogeographic constraints, western rainforest refugia, riverine barriers, montane refugia, and watershed positions, which are all shaped by past climate shifts (reviewed in Vences et al. 2009).

The composition and diversity of communities are also structured by processes that operate at a variety of spatial scales (Borcard et al. 2004; Chase and Myers 2011; Leibold et al. 2004; Wiens 1989). Regional diversity patterns are the result of local processes, underlying environmental heterogeneity, and species dispersal (Ricklefs and Schluter 1993), and at larger spatial scales differences in geographic ranges, biological regions (Morris 2005) and the prevalence of biogeographic barriers (cf. Lomolino and

Davis 1997). At the local scale, interactions and niche-based processes (competition and direct interactions) operate (cf. Harrison and Cornell 2008). However, interspecific competition can also influence large-scale variation in species co-occurrence patterns (e.g., Beaudrot and Marshall 2011; Beaudrot et al. 2013c; Kamilar and Ledogar 2011). Studies of community assembly therefore need to employ spatially explicit methods of analysis that account for the varying contributions of spatial scale (Borcard et al. 2004).

Previous tests of primate community assembly have shown that patterns vary across regions in the relative contribution of environmental and spatial effects, operating at local and regional scales. In the neotropics, Africa, and Borneo, dispersal limitation by distance (a spatial effect) better explains primate community assembly than environmental variables (Beaudrot and Marshall 2011; Gavilanez and Stevens 2013; Kamilar 2009), whereas in Madagascar environmental variables better explain patterns in primate composition than spatial effects (Beaudrot and Marshall 2011). Differences in patterns of community assembly may exist due to intrinsic differences between geographic areas (i.e. climate, biogeography and evolutionary history) and/or the compounding effects of spatial and temporal scale. However, previous community assembly work in Madagascar (Beaudrot and Marshall 2011; Muldoon and Goodman 2010) has not tested the role of biogeographic barriers in shaping community composition, although Madagascar's mammal communities evolved in situ within a biogeographic framework (*sensu* Vences et al. 2009). Madagascar is characterized by regionally pronounced and locally steep environmental gradients, patterns of microendemism across taxa and numerous evolutionary radiations, making it an ideal location within which examine the roles of deterministic, stochastic and biogeographic processes (Vences et al. 2009).

Previous research on primate community assembly focused on primates alone rather than the broader community (e.g., Beaudrot and Marshall 2011; Ganzhorn 1999; Gavilanez and Stevens 2013; Kamilar and Muldoon 2010; but see Beaudrot et al. 2013a, 2013b, 2013c; Muldoon and Goodman 2010), even though primates interact with species from other clades (e.g., Emmons et al. 1983; Ganzhorn 1999; Gautier-Hion et al. 1980). A more inclusive study of all nonvolant mammal communities would not only encapsulate more ecological interactions and functional adaptations to environments, it would provide a more comprehensive understanding of species co-occurrence and biodiversity patterns. Previous research on birds, fish, plants, and invertebrates suggested that body size, dispersal limitation, environmental associations, and biogeographic barriers all influence community assembly (Cottenie 2005; Soininen et al. 2007). These different assembly processes often interact to result in non-random patterns of taxonomic and functional organization.

In this study I use a variation partitioning approach to evaluate the influence of environmental effects, spatial effects and the dispersal costs of biogeographic barriers in shaping patterns of nonvolant mammal community composition in 34 protected areas across Madagascar. Environmental effects, through species-environment sorting, promote species coexistence (Chase and Leibold 2003; Tilman and Pacala 1993). Assuming species are primarily stenoecious (restricted to specific habitats), variation in vegetation (i.e., environmental heterogeneity) is often an important component in community assembly and largely driven by climatic conditions (e.g., Ackerly 2003). Consequently, I use climatic variables, including precipitation and temperature to represent environmental effects. Spatial effects (including dispersal limitation) result in spatially structured patterns independent of environmental heterogeneity (Fortin and Dale 2005; Lindo and

Winchester 2009). Dispersal limitation occurs when a species cannot colonize another area because the new site is too far away (Chase 2003; Condit et al. 2002; Potts et al. 2002; Tuomisto et al. 2003). Here, I model spatial effects with principal coordinates of neighbour matrices, a scale-explicit method for investigating spatial relationships between communities (Borcard et al. 2004). For biogeographic effects I use a ratio of the effective dispersal distance around biogeographic barriers (permanent water bodies, rivers, and the island edge) to the straight-line distance between sites; thereby accounting for the unique contribution biogeographic barriers pose on dispersal.

Additionally, I divide the nonvolant mammal communities into different evolutionary lineages, i.e., primate and non-primate (afrosoricidans, carnivorans, and rodents)) and different functional groups (arboreal and terrestrial species). Arboreal species require varying degrees of intact forest, and this forest-dependence may compound the roles of dispersal limitation by distance and by biogeographic barriers if the matrix between sites is impassable (Pozo-Montuy et al. 2011; Santos-Filho et al. 2012). Groups that are arboreally constrained (most primate species), and therefore limited by long-distance dispersal opportunities, will have community structures that are dependent on the distance between sites (Lindo and Winchester 2009). Madagascar is shaped by severe forest fragmentation (DeFries et al. 2005; Harper et al. 2007), and the matrix between forested sites may be difficult for arboreal species to pass through (e.g., Prugh et al. 2008). Consequently, I predict spatial effects and biogeographic barriers shape primate communities and arboreal communities more than environmental effects. By contrast, groups which are capable of dispersing long distances (non-primates and terrestrial species) are not limited by distance but are instead limited by habitat availability and environmental conditions (Lindo and Winchester 2009). Consequently, I

predict environmental effects best explain non-primate mammal communities and terrestrial communities.

METHODS

Community Composition

I collected data for 34 protected areas in Madagascar (Figure 2.1). I compiled occurrence data for species (orders Afrosoricida, Carnivora, Primates, Rodentia) from published sources of confirmed sighting data to assess the composition of nonvolant mammal assemblages in Madagascar. I used Mittermeier et al.'s (2010) taxonomy for primates and Wilson and Reeder's (2005) taxonomy for non-primates (Table A.1) at the species level. I excluded domesticated and non-indigenous species from assemblage lists. I defined an ecological community as all the nonvolant mammal species that potentially interact within a single patch or local area of habitat (Chase and Leibold 2003; Fauth et al. 1996), in this case protected areas in Madagascar (ranging from 104 km^2 to 5,899 km^2). I identified each species as habitually terrestrial or arboreal based upon descriptions in the primary literature (Table 2.1; Table A.6). Those species that are habitually both arboreal and terrestrial (spend almost equal amounts of time on either substrate type) were included in both terrestrial and arboreal analyses (Table 2.1).

Quantifying Macroecological Effects Related to Community Assembly

Environmental effects

I used georeferenced data on environmental variables for each study site were collected from the Madagascar Digital Elevation Model (CGIAR-SRTM data aggregated to 30s) (Hijmans et al. 2004) and the WorldClim Global Climate Database (Hijmans et al. 2005). Environmental variables were chosen that influence the distribution of plant

species and the productivity of environments. Plant communities in most habitats determine the physical structure of the environment and consequently influence the distributions and interactions of vertebrate species (reviewed in Lawton 1983; McCoy and Bell 1991), including primates (reviewed in Kamilar and Beaudrot 2013; Reed and Bidner 2004). These bioclimatic variables included elevation, mean annual temperature, mean diurnal range in temperature, isothermality, temperature seasonality, maximum temperature (of warmest month, of coldest month), temperature annual range, mean temperature (of wettest quarter, of driest quarter, of warmest quarter, of coldest quarter), precipitation (annual, of wettest month, of driest month, of wettest quarter, of driest quarter, of warmest quarter, or coldest quarter), and precipitation seasonality. I calculated mean values for each environmental variable across a 10 km radius around each study site centroid to ensure that mean values were representative of the protected area, while still being enclosed by the protected area boundaries. Environmental variables were tested for significant autocorrelations (*sensu* Beaudrot and Marshall 2011) using Pearson's product-moment correlation coefficient. To minimize over-fitting models due to highly correlated environmental variables, I included variables in the analysis if they had a correlation of less than 0.8 and documented influences on mammal populations (Table 2.2, Figure 2.2).

Spatial effects

I used principal coordinates of neighbour matrices (PCNM) for the analysis of spatial effects across various spatial scales in the community composition data (Dray et al. 2006). The PCNM approach works well with presence/absence data and community data from multiple sites across space (Legendre et al. 2005). Furthermore, it can be used to detect significant correlations of community composition with environmental variables

independent of spatial autocorrelation at a variety of spatial scales (Borcard and Legendre 2002; Borcard et al. 2004), which is important with geographically distributed data (Fortin and Dale 2005; González-Megías et al. 2005).

PCNM analysis creates spatial predictors that can be directly included in regression models by computing eigenfunctions of spatial connectivity matrices (Griffith and Peres-Neto 2006). PCNM uses a principal coordinate analysis of Euclidean distance matrix among study sites. The analysis truncates each matrix at the smallest distance between nearest neighbours that keeps all sites connected in a single network (~26 km). The eigenvectors (PCNMs) that modelled positive spatial correlation (Moran's I larger than expected value of Moran's I) were retained and used to represent spatial structuring in patterns of community composition. The first PCNMs represent broad scale spatial structures, with successive PCNMs representing progressively smaller spatial scale effects (Borcard and Legendre 2002), ranging between 1400 km (broadest scale) to 26 km (smallest scale). Consequently, PCNMs with positive eigenvectors were evenly separated into small, medium and broad spatial scales to reflect the spatial grain of the study sites (*sensu* García et al. 2010). The use of the terms "small", "broad", and "medium" scales were defined relative to this particular set of study sites and were constrained by the data's resolution and spatial extent. PCNM variables were created using the R package ''PCNM'' (Legendre et al. 2010), based on geographic coordinates for each study site centroid. I calculated the geographic coordinates from the protected area boundaries (Gerber 2010) in ArcGIS 10.1 (Feature to Point tool) for each site.

Biogeographic effects

Biogeographic effects were measured as an effective distance ratio for each type of biogeographic barrier considered (permanent rivers and bodies of water, elevation

slope, and the island edge; Figure 2.3). Types of biogeographic features that have been previously shown to influence primate and mammal species distributions in Madagascar were included in the analyses (*rivers*: Ganzhorn et al. 2006; Goodman and Ganzhorn 2004a; Pastorini et al. 2003; Pearson and Raxworthy 2009; Vences et al. 2009; Wilmé et al. 2006; *elevation*: Cortes-Ortiz et al. 2003; Goodman and Ganzhorn 2004b; *island edge*: on basis of mammal endemicity in Madagascar; Wilmé et al. 2006; Wright 1999). Data on biogeographic dispersal barriers were extracted from digital maps of Madagascar, including permanent rivers and bodies of water (Lehner and Doll 2004), elevation slope (Hijmans et al. 2004), and the island edge (Hijmans et al. 2004). Elevation slope was divided into four equal categories of 22.5º increments (max of 90º). Least-cost paths (LCP) were calculated as measures of the effective distance between each unique site pair based on the costs of crossing over or around biogeographic barriers. Using the Spatial Analyst extension in ArcGIS version 10.1 (ESRI) and a custom Python script, I performed the LCP analysis in which the path resulting in the lowest cost to reach a target site from the origin site was identified (Figure 2.4). LCPs between sites were measured with a friction layer that depicted the cost of crossing a habitat with biogeographic barriers present. A simple model was used where a prohibitively high cost (cells were set to "NoData" to make them impassable) was assigned to permanent biogeographic barriers (permanent water bodies, permanent rivers, and the island edge) and remaining habitat had no cost assigned to it. The 0º to 45º slope increments were assigned the lowest travel cost (value of 9, on a scale from 1-9 with 9 being the lowest), the 45 to 70.5º increment was assigned a moderate cost (value of 5), and 70.5º to 90º the highest and most prohibitive cost (value of 1). These divisions and assigned costs were chosen to reflect the energetic costs of travelling over terrains with higher travel costs (*sensu* Wade

et al. 1998). Effective distance ratios were then calculated for each site. For n sites numbered 1 to *n*, the effective distance ratio of site *i*, denoted DR*i*, was defined as

Equation 2.1: $\mathrm{DR}i = \sum_{1 \le j \le n, j \ne i} \frac{d^*(i,j)/d(i,j)}{n-1}$,

where $d^*(i, j)$ was the effective distance between sites *i* and *j* and $d(i, j)$ was the Euclidean distance between sites *i* and *j*. This measure reflects the effective distance between sites and degree of site isolation. I conducted this analysis separately for every unique site pair and each type of barrier. Where biogeographic barriers did not exist the Euclidean distance and effective distance was equal (ratio of 1). Where biogeographic barriers imposed travel costs the effective distance was longer than the Euclidean distance and the effective distance ratio was greater than one.

Modeling Macroecological Effects on Community Composition

All analyses were conducted in R 2.15.3. I modeled the multivariate response of Madagascar's (1) nonvolant mammal communities (2) primate communities, (3) non-primate nonvolant mammal communities, (4) arboreal nonvolant mammal communities, and (5) terrestrial nonvolant mammal communities to a matrix of environmental variables, spatial variables (PCNMs) and biogeographic effective distance ratios using variation partitioning techniques. In this modelling approach community composition was the response variable, and the environmental, spatial and biogeographic variable sets were the explanatory variables. Prior to analysis, community composition matrices (species x site) were Hellinger transformed to allow using redundancy analysis (RDA) without considering the common absence of a species as a resemblance between communities (Legendre and Gallagher 2001).

Community composition data were checked for the presence of linear trends (trend between composition and geographic coordinates) using RDA and an ANOVA

with 1000 permutations. A significant trend indicated the presence of spatial effects at broader scales than the sampling extent, or a gradient across the entire studied area (Borcard et al. 2004). Composition should be detrended for PCNM analysis, or a large number of PCNMs would be necessary to model the linear trend in composition and their role in modelling finer spatial scales might go unnoticed (Borcard et al. 2004). Where the linear trend was significant composition was detrended; composition matrices were regressed against longitude and latitude and the residuals retained as response variables (*sensu* Borcard et al. 2004; Legendre and Legendre 2012). Both nondetrended and detrended (where applicable) composition matrices were retained for analysis because including the linear trend in composition (nondetrended) was equivalent to modelling the spatial pattern of composition at the broadest spatial scale (all of Madagascar), while detrending allowed for modelling smaller spatial scales (detrended).

Global models (with complete sets of explanatory variables, Table 2.2) for each community grouping and effect type (location, environmental, biogeographic, spatial) were tested for significance with a RDA and an ANOVA with 1000 permutations, from which the global adjusted R^2 value was calculated. I then used a forward selection procedure to retain the variables (latitude and longitude, PCNMs, environment, biogeographic) with the highest explanatory power while preserving interactions between variables and producing the most parsimonious model (Legendre and Legendre 2012). For each significant global model, a forward selection with 9999 Monte Carlo permutation tests was done, and a double stopping criterion was used where the selection stopped if either a p-value of 0.05 or the global adjusted R^2 were exceeded (Blanchet et al. 2008). I repeated the forward selection process for each variable group and each taxonomic/functional group individually. The RDA and tests of significance were

computed with the "rda" and "anova.cca" functions of the "vegan" library in R (Oksanen et al. 2008), and the "forward.sel" function in the "packfor" package (Dray et al. 2011) was used for forward selection.

Variation partitioning was then used to identify the components of variation in community composition explained by environmental effects, biogeographic barriers, and spatial effects (e.g., Gilbert and Lechowicz 2004; Jones et al. 2008; Kamilar 2009; Legendre et al. 2005; Lindo and Winchester 2009). Variation partitioning was carried out using the "varpart" function of the "vegan" R package (Oksanen et al. 2008), which uses RDA to compute the variation attributable to each set of explanatory variables. I used the adjusted R^2 statistic to assess the proportion of the response variation explained by each explanatory data set and their combinations. The adjusted R^2 provides unbiased estimates of the explained variation (Peres-Neto et al. 2006). Only variables selected in the forward selection procedure were included in the variation partitioning analyses. I used partial RDAs and ANOVAs to test the significance of each pure component of variation while controlling for other variable sets. For example, I tested the amount of variation due to environmental effects for significance while controlling for spatial and biogeographic effects. Where variation was shared between PCNMs and other components of variation (environmental variables and biogeographic effective distance ratios), that component of shared variation was interpreted as spatially structured (*sensu* Laliberté et al. 2009). Dividing the PCNMs into broad, medium, and small spatial scales showed the amount of variation attributed to those spatial scales.

Variation partitioning was run in two ways across the five community groups: Model 1: using forward selected environmental variables, PCNMs (small, medium, broad scale), biogeographic effective distance ratios, and the linear trend of geographic location

(longitude and/or latitude) without detrending composition; and Model 2: using forward selected environmental variables, PCNMs (small, medium, broad scale), biogeographic effective distance ratios, and detrended composition (*sensu* Borcard et al. 2011). Several components of variation are reported: pure effects where the variation was attributable to a single source (e.g., pure environmental effects), total effects where the total amount of variation is attributable to a source and its covariations with other variables (e.g., total environmental effects), and shared spatial-environmental effects (the shared variation of environmental and spatial effects). I considered statistical tests significant at $p < 0.05$.

RESULTS

Patterns of Community Composition

Of 131 nonvolant mammal species in this study, 70 were primates, representing five families, and 15 genera (Table A.6). The remaining 61 non-primate mammals represented three orders (Afrosoricida, Carnivora and Rodentia), three families, and 24 genera (Table A.6). Alpha diversity (the number of species present at each study site) ranged 11-42 species, including 3-13 primates and 5-30 non-primate species at each site. I classified 78 species as arboreal, 43 terrestrial and 10 as habitually both terrestrial and arboreal (Table 2.1).

Significant linear trends between composition and location (latitude and longitude) were present in all five community types: all nonvolant mammals ($F = 6.57$, df $= 2$, $p < 0.001$), primates ($F = 6.44$, df $= 2$, $p < 0.001$), non-primates ($F = 6.45$, df $= 2$, $p < 0.001$), arboreal mammals ($F = 6.19$, df $= 2$, $p < 0.001$), and terrestrial mammals ($F = 6.71$, df $= 2$, $p < 0.001$). Twenty-two PCNMs were present in the datasets with 10 eigenvectors with positive spatial correlations. These 10 eigenvectors represented two

spatial scales: broad (PCNMs 1-5) and medium (PCNMs 6-10) (Figure 2.6). No small-scale spatial structures were positive and/or significant (PCNMs 10-20). PCNM 1 describes a latitudinal gradient in nonvolant mammal community composition, where the north and south of Madagascar are differentiated, and PCNM 2 describes a combination of a latitudinal and longitudinal division between mammal communities in the northeast and those in the southwest (Figure 2.6). All five composition matrices were detrended due to significant linear trends and used for Model 2 analyses.

Biogeographic Effective Distances

Results suggest that biogeographic barriers created additional dispersal costs for species moving between study site locations (Table 2.3) and these costs were dependent on the relative locations of biogeographic barriers. Mean effective distances were highest when travelling over elevation changes (608.18 km), while the lowest were when travelling around permanent water bodies (596.51 km). The ratio of effective distance to Euclidean distance followed a similar pattern. However, the sites that had the highest mean effective distances and the highest ratio differed (Table 2.3).

PCNM Analyses and Forward Selection

Model 1 (nondetrended data)

The global PCNM analyses were significant for all taxonomic groupings: nonvolant mammals (F = 2.91, df = 10, $p < 0.001$), primates (F = 3.53, df = 10, $p < 0.001$), non-primate mammals (F = 2.47, df = 10, $p < 0.001$), arboreal mammals (F = 3.18, df = 10, $p < 0.001$), and terrestrial mammals (F = 2.66, df = 10, $p < 0.001$). For all community groupings, latitude and longitude were significant in the forward selection procedure (Table 2.4 and 2.5), meaning that significant linear trends in community

composition along both latitude and longitude in Madagascar were present. Significant environmental variables were the same for nonvolant mammals, primates and arboreal mammals, although in different orders, and included annual temperature, annual precipitation, temperature seasonality, and precipitation seasonality (Table 2.4 and 2.5). Annual temperature, annual precipitation, temperature seasonality, and elevation significantly described non-primate mammals and terrestrial mammals (Table 2.4 and 2.5). Nonvolant mammals, primates, and arboreal mammals also had the same seven significant PCNMs. These seven PCNMs described both broad and medium scale structures in the community composition (Figure 2.5). Terrestrial mammals and primates had the same four significant PCNMs depicting broad scale structuring of compositional patterns. The biogeographic effective distance ratio accounting for the cost of travelling within the island edge was significant for all five taxonomic groupings.

Model 2 (detrended composition data)

The global PCNM analyses were significant for all nonvolant mammals (F = 1.34, df = 10, p = 0.006), primates (F = 1.82, df = 10, p < 0.001), and arboreal mammals (F = 1.62, df = 10, p < 0.001), and non-significant for non-primate mammals (F = 1.02, df = 10, p = 0.407) and terrestrial mammals (F = 1.13, df = 10, p = 0.183). All mammals had three significant PCNMs, and primates and arboreal mammals had four significant PCNMs at both broad and medium spatial scales (Table 2.4 and 2.5). Since the global PCNM models were not significant for non-primate and terrestrial mammals, forward selection of variables was not performed (Table 2.4 and 2.5). No biogeographic effective distance ratios were forward selected for the detrended composition data. For all community groupings, elevation was the only significant variable for detrended community data.

Variation Partitioning

Model 1 (nondetrended data)

Environmental and spatial (PCNMs) variables significantly shaped nonvolant mammal communities, while geographic location and biogeographic barriers (effective distance ratio) played less important and non-significant roles (Figure 2.7, Table 2.4). I excluded biogeographic barriers from the variation partitioning models explained below due to non-significant and very small contributions to nondetrended community composition for all groups. Instead, the variation partitioning models included environmental effects, geographic location, broad scale PCNMs and medium scale PCNMs (Figure 2.7, Table 2.4 and 2.5). Of the explained variation, pure spatial (7.3%), pure environmental (7.0%), and shared environmental and broad scale spatial effects (7.2%; Figure 2.7; Table 2.4) shaped nonvolant mammals almost equally. Of the spatial effects, broad scale (3.7%) and medium scale (3.6%) proportions of variation were almost equal (Table 2.4). Location explained a small portion of nonvolant mammal communities (2.0%). Primate and arboreal mammal communities had more of their explained variation due to spatial effects (11.2%, 9.8%, respectively) than environmental effects (5.7%, 7.5%, respectively), and broad scale effects (6.0%, 5.1%, respectively) explained similar amounts of variation to medium scale effects (5.2%, 4.7%, respectively; Table 2.4 and 2.5). Additionally, covarying effects, with 8-10% of compositional variation explained by joint broad scale spatial and environmental effects, explained most of the variation by environmental and spatial effects in primate and arboreal mammals (Table 2.4 and 2.5). Only 2.3% and 2.0% of the variation in primate and arboreal mammal communities respectively was due to location. For non-primate and terrestrial mammals spatial effects explained a very small and non-significant proportion

of variation (1.3%, 1.8%, respectively), with environmental effects (12.4%, 10.8%, respectively) explaining six and five times more of the variation, respectively (Table 2.4 and 2.5). The combined environmental and spatial variation in non-primate (2.5%) and terrestrial mammal communities (3.7%) was a small part of the total variation explained by the model (Table 2.4 and 2.5). Non-primate and terrestrial mammals had 2.5% and 1.8% (not significant) of their variation respectively due to location, which was greater than the contribution of spatial broad scale effects for both groupings. Across groups primate and arboreal mammal models explained the largest proportion of nondetrended community composition (range = 48.9%-50.1% explained variation; Figure 2.7; Table 2.4 and 2.5).

Model 2 (detrended composition data)

The variation partitioning models for detrended community compositions did not include biogeographic effective distance ratios because none were significant. Furthermore, only one environmental variable (elevation) was significant (Table 2.4 and 2.5). Model fit for Model 2 was lower than for Model 1, explaining 8.3-18.1% of community variation (Figure 2.8, Table 2.4 and 2.5). Pure spatial effects versus environmental effects explained the greatest proportion of variation for all nonvolant mammals (7.5% vs. 2.6%), primates (15.1% vs. 0.7% (non-significant)) and arboreal mammals (12.9% vs. 2.6%). Conversely, the pure environmental effect of elevation was the only variable explaining community variation for non-primates (6.8%) and terrestrial mammals (6.5%). The variation partitioning for all nonvolant mammals, primates and arboreal mammals across medium and broad scales had similar patterns. The PCNMs representing broad scales explained almost twice the variation in community composition than those at medium scales. Furthermore, the total variation explained by broad scale

structuring of composition was two to three times that of medium scale for analyses of all mammals, primates and arboreal mammals (Figure 2.8, Table 2.4 and 2.5).

DISCUSSION

Environmental and spatial effects almost equally shaped nonvolant mammal communities in Madagascar. Contrary to predictions, biogeographic barriers, measured as effective dispersal distance ratios, did not significantly shape any community. As predicted, however, variation in primate and arboreal mammal communities was mostly due to spatial effects. In addition, environmental effects explained all of the compositional variation for non-primate and terrestrial mammals. These results provide support for functional differences between taxonomic groups as important considerations in the study of community assembly.

Previous community assembly research in Madagascar found that Madagascar's primate (Beaudrot and Marshall 2011; Kamilar 2009) and nonvolant mammal communities (Muldoon and Goodman 2010) sort with environmental variables. However, a significant distance effect in the mammal communities across the island also existed (Muldoon and Goodman 2010). Regardless of geographic location (i.e. longitude and latitude), this study shows that nonvolant mammal community composition is shaped by spatial effects occurring at broad and medium spatial scales, and the contribution of these spatial effects is equal to the contribution of environmental effects.

Madagascar has substantial environmental gradients with high climate variability (Dewar and Richard 2007). In this study, environmental effects were weakly related to medium spatial scales and strongly related to broad scales. The climatic variables that were forward selected (*not detrended*: precipitation and temperature; *detrended*: elevation) are broad scale features that characterise ecoregional differences in

Madagascar (Dewar and Richard 2007; Donque 1972; Muldoon and Goodman 2010). Eastern Madagascar has the most rain due to orographic precipitation, whereas the west is hotter and drier (Jury 2003). Differences in community composition in nonvolant mammal communities are therefore not only characterized by geographic distance (Muldoon and Goodman 2010, and this study) but also by differences in broad scale environmental variables, such as precipitation (Kamilar and Muldoon 2010; Muldoon and Goodman 2010; and this study). Furthermore, patterns of temperature and precipitation seasonality were significant factors shaping all nonvolant mammals (*sensu* Dewar and Richard 2007) when not detrended. The observation that precipitation and rainfall were not significant variables when community composition was detrended (effect of location removed) and spatial effects were better explanations for patterns in community composition further supports the importance of ecoregional differences driving community assembly in Madagascar.

Primates and Arboreal Mammals vs. Non-primates and Terrestrial Mammals

Overall, primate communities and arboreal communities were very similar because primates made up more than 88% of arboreal community diversity. Spatial effects strongly shaped both primates and arboreal mammal communities but biogeographic effects were not significant. Because all primate species in Madagascar are at least somewhat arboreal, spatial effects similarly shaped primates and arboreal mammals. Interestingly, spatial effects explained more of the variation in composition for primates than arboreal mammals. Primates in Madagascar have on average larger body sizes ($\bar{x}$ = 1713g ± 1967g) and are potentially more restricted in their habitat requirements than the smaller bodied arboreal non-primate mammals ($\bar{x}$ = 970g ± 2582g, Table 2.1). Larger bodied arboreal animals require larger substrates for travel and support

(*sensu* Remis 1995; Warren and Crompton 1998), additionally constraining their distribution and affecting the assembly processes most likely to affect their community composition. However, recent work has shown that body mass is phylogenetically conserved in Malagasy primates and not shaped by environmental variables or space (Kamilar et al. 2012). Body size might not be driving the importance of spatial effects in primate and arboreal mammal communities. Instead, habitat dependence on resources, including food availability, may drive this pattern. Madagascar's primates have flexible ecological requirements (e.g., Kamilar 2009; Kamilar and Muldoon 2010; Kamilar et al. 2012), with unique suites of adaptations (e.g., low basal metabolic rates, unusual life-history patterns, small group sizes) to high climatic variability (reviewed in Dewar and Richard 2007). In this study both temperature and precipitation seasonality, when not detrended, significantly shaped primate and arboreal mammal communities. It is possible that primate ecological flexibility dampens the importance of environmental effects in comparison to the contribution of spatial effects on primate and arboreal mammal communities.

In contrast to primate and arboreal mammal communities, only environmental effects explained non-primate mammal and terrestrial mammal communities. Non-primate mammal and terrestrial mammal communities had very similar species composition, because non-primate species made up 98% of the diversity in terrestrial communities. Elevation was a significant environmental variable for non-primate and terrestrial mammals in both models (nondetrended and detrended) while it was only significant for detrended composition in primate communities. Elevation is a previously documented important environmental variable for mammals in Madagascar (e.g., Goodman et al. 1996; Goodman et al. 1999; Goodman and Rasolonandrasana 2001). In

addition, climatic trends in small mammal diversity exist with peaks occurring with mountain height (McCain 2005). Small mammals are potentially responding to a climatic optimum, which may exist below the persistent cloud cover at the top of mountains (Goodman et al. 1999; McCain 2005). The absence of elevation slope changes and the presence of elevation, precipitation, and temperature as significant environmental variables shaping non-primate and terrestrial mammal communities suggest that the climatic features associated with elevation are helping shape community composition. The contribution of elevation to patterns of community composition may also result from historical patterns of allopatric speciation, due to population isolation in river watersheds of different elevational ranges during Quaternary climate change (Wilmé et al. 2006). Evidence of such allopatric speciation exists for diurnal primates (Wilmé et al. 2006), but has had mixed support in other fauna (e.g., *Eliurus myoxinus*: Shi et al. 2013, reptiles: Pearson and Raxworthy 2009).

The finding that spatial effects were more important to primates and arboreal mammals than to terrestrial and non-primate mammals is not surprising because habitat requirements restrict arboreal animals (of which most were primates). Grassland edged with diverse woodlands covers (at least) seventy two percent of Madagascar (de Wit 2003). Consequently, the distance between sites and the nature of the matrix between protected areas probably place different demands on dispersing species. In Madagascar, a country shaped by marked habitat change over the last 2000 years and severe forest fragmentation (DeFries et al. 2005; Harper et al. 2007), arboreal species are predicted to be highly dispersal limited because the matrix between forested sites may be difficult to pass through (e.g., Prugh et al. 2008). Furthermore, the central highlands of Madagascar present a significant barrier to faunal dispersal (Muldoon and Goodman 2010). A matrix

of anthropogenic habitat between sites is probably unsuitable for most Malagasy primate species (Schwitzer et al. 2011), although some species, such as *Microcebus* and *Mirza*, thrive in anthropogenic habitats (e.g., Ganzhorn 1987; Ganzhorn et al. 1999; Irwin et al. 2010). Furthermore, primate (and reptile) dispersal in Madagascar is highly geographically constrained, and most species are endemic to only 25% of Madagascar's surface area (Pearson and Raxworthy 2009).

Biogeographic Barriers

My measure of site isolation (biogeographic effects) did not explain patterns in community composition regardless of taxonomic grouping. In addition to the potential error in assigning cost values to barriers used to generate dispersal surfaces, this unexpected finding has three possible explanations. First, the effect of rivers and water bodies as biogeographic barriers may be too species-specific to see at a community level and biogeographic effective distance had an averaging effect by looking at entire communities. Rivers are biogeographic dispersal barriers for a variety of Malagasy species when investigating species range limits (reviewed in Goodman and Ganzhorn 2004b). However, my community level of analysis may have subsumed species level variation in biogeographic barriers. For example, several *Eulemur* species are not affected by rivers and have ubiquitous distributions, while other lemur genera including *Indri* and *Propithecus* (some species) are biogeographically constrained by the position and size of some rivers (Goodman and Ganzhorn 2004a). Furthermore, detailed survey data in a variety of habitat types is lacking for many species (Goodman and Ganzhorn 2004a), limiting documented environmental and biogeographic limits of many species. A useful avenue for future research would be to evaluate both the taxonomic and functional

(e.g., body size or locomotion) specificity of dispersal costs around biogeographic barriers.

Second, by considering all permanent water bodies, as opposed to those that have already been supported as important biogeographic barriers (e.g., Bemarivo River, Lokoho River, Antainambalana River, Mangoro River, Mananara River; reviewed in Goodman and Ganzhorn 2004a), my analysis may have concealed the effect of the few and significant biogeographic barriers that exist. These previously established important biogeographic barriers may be unique in their size, elevational distribution, and position of their sources or headwaters (*sensu* Goodman and Ganzhorn 2004ba; Wilmé et al. 2006). Although, these rivers potentially constrained the distribution of species thousands of years ago, today they might not be the strongest contributors to mammal distributions in Madagascar.

Third, the ecological history of Madagascar is under debate. The assumption that primary forest covered Madagascar prior to human arrival is contested (e.g., Burney et al. 2003; Klein 2002; Muldoon et al. 2012). Either Madagascar was a forest-woodland-grassland mosaic (Burney 1997; Muldoon et al. 2012) that shifted to grasslands by the action of fires (Burney 1996), or a forested corridor existed westward across the southern part of the highlands, allowing for faunal dispersal (reviewed in Muldoon et al. 2012). The compositional differences in mammal communities between east and west Madagascar is suggested as evidence of past faunal exchange across the Central Highlands (Muldoon and Goodman 2010), resulting in damped differences between community composition. Moreover, terrestrial fauna may have dispersed more easily than arboreal fauna, accounting for the lack of spatial effects detected in the community composition for non-primates and terrestrial mammals. The biogeographic complexity

and varying patterns of faunal endemism in Madagascar make recovering highly congruent patterns of vicariance events unlikely (Pearson and Raxworthy 2009), and may limit the ability of a single index to reveal salient patterns in community composition.

Although previous research considered the distance between sites or the spatial characteristics of a biogeographic area as indicators of historical, regional or biogeographic processes acting (e.g., Beaudrot and Marshall 2011; Kamilar 2009), the relationship between distance and historical and biogeographic process is unclear. PCNMs are suggested good proxy measures for historical events in Neotropical primates that may also represent the role of dispersal limitation by distance (Gavilanez and Stevens 2013). Furthermore, a measure of dispersal limitation (as geographic distance) can be the result of both stochastic dispersal limitation and historical/biogeographic processes due to variation in dispersal ability or speciation among taxa resulting in a geographic distance effect in taxonomic patterns of primate communities (Kamilar 2009). However, investigating spatial effects and biogeographic barriers as separate entities can help identify the variation in community structure that is separately due to dispersal limitation, additional spatial effects, and biogeographic barriers. Using a scale explicit approach for investigating assembly can help reveal the relative importance of each process against a complex background of processes operating at various spatial scales (Chase and Myers 2011). Although neither the biogeographic effective distance ratios, nor the shared spatial-biogeographic variation explained patterns of composition in this study, the study of different barriers (refugia and watersheds, *sensu* Vences et al. 2009), barrier metrics, different groups, or different biogeographic regions may consequently reveal greater contributions of biogeographic processes to community assembly.

Methodological Challenges

The absence of small spatial scale structures in this data is potentially due to the scale at which I was able to describe the communities. Because they were the total species composition of an entire protected area, the sampling may be at too large a grain to account for fine scale spatial patterns. The absence of these fine scale structures highlights the need for more detailed surveys within more protected areas to account for local scale processes that may be shaping composition, including inter- and intra-specific competition (e.g., Kamilar and Ledogar 2011).

The amount of explained variation in community composition in this study was between six and 50%, leaving large amounts of community variation unexplained. Separating the co-varying effects of community assembly processes requires further elucidation of the biogeographic and environmental variables that influence them. Additionally, pure spatial effects may hide unmeasured spatially structured environmental or deterministic variables (Borcard and Legendre 1994; Jones et al. 2008). A further possibility is that the variables I initially selected may not be ideal for detecting community assembly processes in mammal communities. While unexplained variation can highlight hidden variables, a high unexplained fraction of variation is likely common in ecological data (ter Braak and Prentice 1988). Furthermore many other studies have also found large unexplained fractions (range = 20 to 49%) (e.g., Cottenie 2005; Gavilanez and Stevens 2013; Gilbert and Lechowicz 2004; Jones et al. 2008).

Conclusions

Community assembly is complex, and processes are not mutually exclusive. Instead of being generalizable by taxa, functional traits (e.g., arboreal vs. terrestrial) may better describe patterns in community assembly. In this study, variables used to indicate

the operation of deterministic, stochastic, and biogeographic processes differentially shaped terrestrial mammal communities from arboreal mammal communities. Spatial effects best explained arboreal mammal communities (and primates), whereas terrestrial mammal communities (and non-primate mammals) were best explained by environmental effects. Future studies and comparisons of Madagascar's primate communities may benefit from trait-specific analyses of ecological processes because niche differences, which stem from trait-level differences, shape deterministic processes. The role of spatial effects were shown here to be more important to arboreal fauna than terrestrial fauna; a logical result if the extant matrix between sites in Madagascar is impassable, and is also a potential by-product of severe habitat disturbance. This difference in the relative contribution of community assembly processes to different taxonomic groupings highlights an alarming conservation concern for the arboreal mammals and primates of Madagascar because continued habitat modification is likely to impact their dispersal. Research is needed to identify the unique contribution anthropogenic disturbance has on patterns of community assembly because predictive models for future community-level changes with continued land modification are required for evidence-based conservation and management practices.

Note: This chapter has been modified from its published version, see Bannar-Martin 2014.

Table 2.1. Species richness for each nonvolant mammal order in Madagascar reported in this study, including assignments to terrestrial and/or arboreal groups and adult body mass statistics.

Order	**Terrestrial**	**Arboreal**	**Arboreal & Terrestrial**
Primates	0	69	1
Adult Body Mass (g)[a]			
Mean ± SD		1713.50±1967.16	2640
Range		48.50-8650	
Afrosoricida	25	0	4
Carnivora	5	0	3
Rodentia	13	9	2
Adult Body Mass (g)[a]			
Mean ± SD	332.20±637.47	970.20±2582.08	1843.34±3436.10
Range	3.4-2800	8.08-9500	8.08-9500

[a] Adult body mass data obtained from PanTHERIA (Jones et al. 2009) for 70 of the 131 species present in this study.

Table 2.2. Variables tested for significant relationships with community composition in this study. All variables were included in each global model for each community grouping (primates, non-primate mammals, arboreal mammals, terrestrial mammals) and each effect type (location, environmental, biogeographic, spatial), followed by a forward selection procedure to select variables for reduced models.

Location	Environmental Effects[1]	Biogeographic Effects	Spatial Effects
• Longitude • Latitude	• Elevation • Mean annual temperature • Temperature seasonality • Annual precipitation • Precipitation seasonality	• Elevation effective distance ratio • Permanent water bodies and rivers effective distance ratio • Island edge effective distance ratio	• Broad Scale (PCNMs 1 to 5) • Medium Scale (PCNMs 6-10)

[1] Variables shown here are those with Pearson's product-moment correlation coefficient of less than 0.8. Selected from the following set of environmental variables: elevation, mean annual temperature, mean diurnal range in temperature, isothermality, temperature seasonality, maximum temperature (of warmest month, of coldest month), temperature annual range, mean temperature (of wettest quarter, of driest quarter, of warmest quarter, of coldest quarter), precipitation (annual, of wettest month, of driest month, of wettest quarter, of driest quarter, of warmest quarter, or coldest quarter), and precipitation seasonality.

Table 2.3. Comparison of straight line (Euclidean) and biogeographic effective distances (including biogeographic barriers) between 34 study sites in Madagascar. Site averages, calculated from a site-by-site distance matrix, are presented. The biogeographic effective distance ratio is the ratio of each biogeographic effective distance to the Euclidean distance. It is a measure of how isolated a site is, and considers the unique role different biogeographic barriers have on the effective dispersal distance between sites.

	Euclidean distance (km)	**Island edge**	**Permanent Water bodies**	**Elevation changes**
		Biogeographic effective distances (km)		
Mean ± SD	562.76±94.95	598.48±102.05	596.51±101.28	608.18±104.82
Range	434.16-794.96	461.79-843.90	460.84-847.66	467.35-862.17
		Biogeographic effective distance ratios		
Mean ± SD		1.06±0.015	1.06±0.015	1.08±0.020
Range		1.05-1.12	1.03-1.11	1.06-1.13

Table 2.4. Variation partitioning of community composition attributed to environmental effects (climate and elevation), spatial effects (PCNMs), and biogeographic barriers (biogeographic effective distance ratios) using partial redundancy analysis. Two components of variation are reported (as percentages): pure variation (the amount of variation only attributable to that source), and total variation (the amount of variation in total attributable to that source, including its covariations with other variables, shown in parentheses). Significant forward selected variables from each source of variation are included in the order of their contribution. Sources that were not significant once the data were detrended were not analysed. Asterisks indicate significant components of pure variation: $p < 0.001$***, $p < 0.01$**, $p < 0.05$*.

	All mammals		Primates		Non-primates	
Source	**Variables**	**Variation**	**Variables**	**Variation**	**Variables**	**Variation**
Model 1 (including linear trend)						
Geographic location	Long, Lat	2.0* (25.2)	Long, Lat	2.3* (24.8)	Long, Lat	2.5* (24.8)
Environmental effects	AT, AP, TS, PS	7.0** (34.9)	AP, AT, TS, PS	5.7** (33.7)	AT, AP, TS, Elev	12.4** (36.9)
Biogeographic barriers [a]	EdgeDR	<1	EdgeDR	<1	EdgeDR	<1
Spatial effects[b] (all scale PCNMs[c])		7.3		11.2		1.3
Broad scale spatial effects	2,1,3,5,4	3.7** (30.6)	2,1,3,5,4	6.0** (35.4)	2,1,5,4	1.3 (27.0)
Medium scale spatial effects	6,7	3.6** (1.9)	6,7	5.2* (3.3)		
Environmental effects + location		0.6		<0		<0
Environmental + broad scale spatial effects		7.2		10.2		2.5
Environmental + medium scale spatial effects		<0		<0		
Total explained variation in model		44.9		50.1		41.1

Table 2.4 (continued)

	All mammals		Primates		Non-primates	
Source	**Variables**	**Variation**	**Variables**	**Variation**	**Variables**	**Variation**
Model 2 (detrended composition data)						
Environmental effects	Elev	2.6* (5.2)	Elev	0.7[ns] (3.7)	Elev	6.8**[d]
Spatial effects [b] (all scale PCNMs[c])		7.5		15.1		
Broad scale spatial effects	4,2	3.8** (6.0)	4,2,3	10.8** (13.1)	4	
Medium scale spatial effects	6	2.2** (2.0)	6	4.2** (3.5)		
Environmental + broad scale spatial effects		2.6		3.1		
Environmental + medium scale spatial effects		0.2		0.1		
Total explained variation		12.5		18.1		6.8[d]

Abbreviations: Long: longitude; Lat: latitude; AT: mean annual temperature; TS: temperature seasonality; AP: annual precipitation; PS: precipitation seasonality; Elev: elevation; EdgeDR: island edge effective distance ratio; NS: not significant.

[a] Not tested because variation partitioning can only have a maximum of four explanatory matrices, and in the overall global RDA model biogeographic processes' contribution to variation in composition was minor.

[b] Combined variation of the pure broad scale effects and pure medium scale effects, consequently significance is not shown.

[c] Eigenvectors from the principal coordinate analysis of the neighbour matrix (PCNM) based on the Euclidean distance between site centroids.

[d] Adjusted R^2 value from the global RDA for environmental effects because no other variable sets were significant, and consequently did not undergo the forward selection procedure.

Table 2.5. Variation partitioning of functional community groups (see Table A.6) attributed to environmental effects (climate and elevation), spatial effects (PCNMs), and biogeographic barriers (biogeographic effective distance ratios) using partial redundancy analysis. Two components of variation are reported (as percentages): pure variation (the amount of variation only attributable to that source), and total variation (the amount of variation in total attributable to that source, including its covariations with other variables, shown in parentheses). Significant forward selected variables from each source of variation are included in the order of their contribution. Sources that were not significant once the data were detrended were not analysed. Asterisks indicate significant components of pure variation: $p < 0.001$***, $p < 0.01$**, $p < 0.05$*.

	Arboreal mammals		**Terrestrial mammals**	
Source	**Variables**	**Variation**	**Variables**	**Variation**
Model 1 (including linear trend)				
Geographic location	Long, Lat	2.0* (24.0)	Long, Lat	1.8 (25.7)
Environmental effects	AP, AT, TS, PS	7.5** (35.1)	AT, AP, TS, Elev	10.8** (37.2)
Biogeographic barriers [a]	EdgeDR	<1	EdgeDR	<1
Spatial effects [b] (all scale PCNMs [c])		9.8		1.8
Broad scale spatial effects	2,1,5,4,3	5.1** (31.9)	2,1,5,4	1.8 (29.4)
Medium scale spatial effects	6,7	4.7** (4.0)		
Environmental effects + location		0.2		<0
Environmental + broad scale spatial effects		8.3		3.7
Environmental + medium scale spatial effects		<0		
Total explained variation		48.9		42.0

Table 2.5 (continued)

Source	Arboreal mammals		Terrestrial mammals	
	Variables	**Variation**	**Variables**	**Variation**
Model 2 (not including linear trend)				
Environmental effects	Elev	2.6* (5.6)	Elev	6.5*[d]
Spatial effects [b] (all scale PCNMs [c])		12.9		
Broad scale spatial effects	4,2,3	8.3** (10.4)		
Medium scale spatial effects	6	4.6** (4.2)		
Environmental + broad scale spatial effects		2.9		
Environmental + medium scale spatial effects		0.4		
Total explained variation in model		18.0		6.5[d]

Abbreviations: Long: longitude; Lat: latitude; AT: mean annual temperature; TS: temperature seasonality; AP: annual precipitation; PS: precipitation seasonality; Elev: elevation; EdgeDR: island edge effective distance ratio; NS: not significant.

[a] Not tested because variation partitioning can only have a maximum of four explanatory matrices, and in the overall model biogeographic processes' contribution to variation in composition was minor (less than 1%).

[b] Combined variation of the pure broad scale effects and pure medium scale effects, consequently significance is not shown.

[c] Eigenvectors from the principal coordinate analysis of the neighbour matrix (PCNM) based on the Euclidean distance between site centroids.

[d] Adjusted R^2 value from the global RDA for environmental effects because no other variable sets were significant, and consequently did not undergo the forward selection procedure.

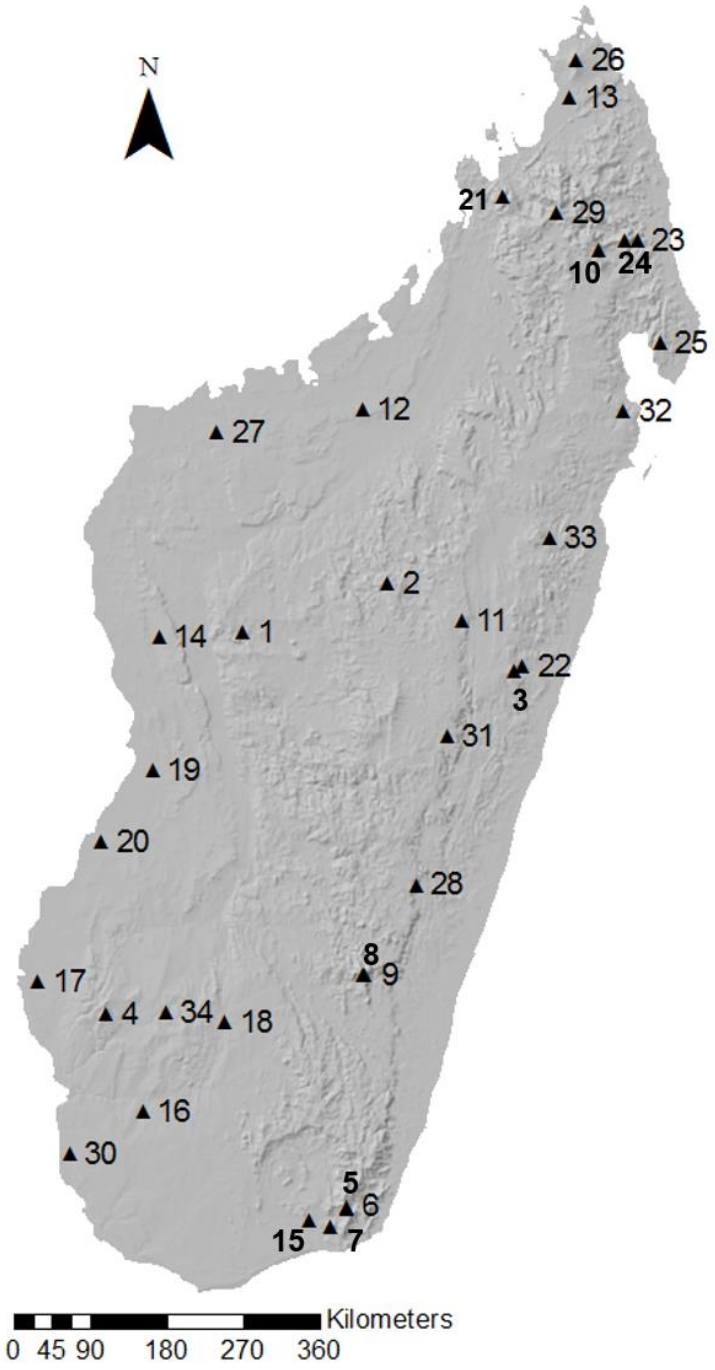


Figure 2.1. Locations of study sites in Madagascar included in this study. Elevation is depicted as a hillshade. Names of the numbered sites are in Table A.1.

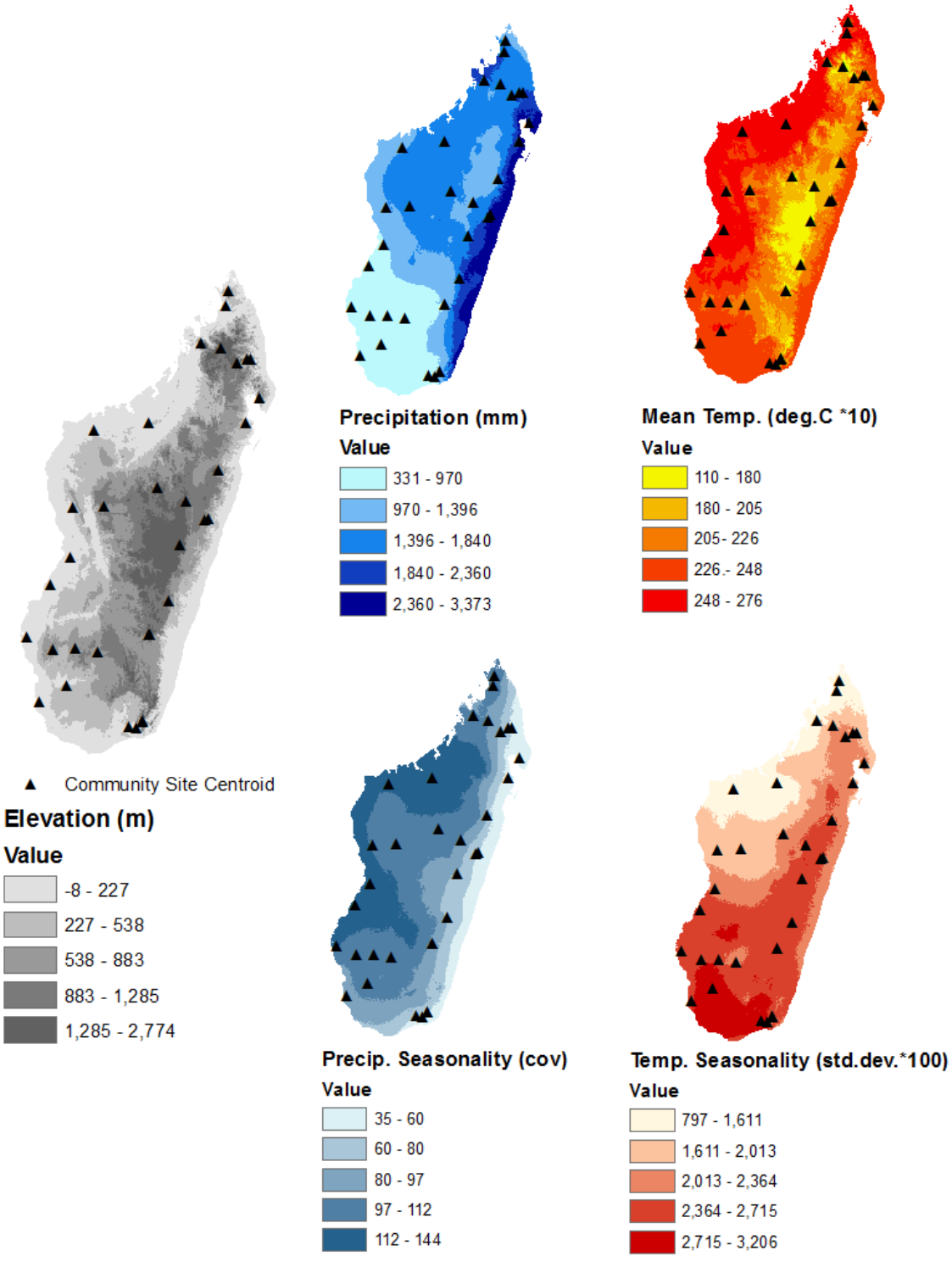


Figure 2.2. Environmental variables across Madagascar. Values are divided by natural breaks (Jenks) for visual clarity.

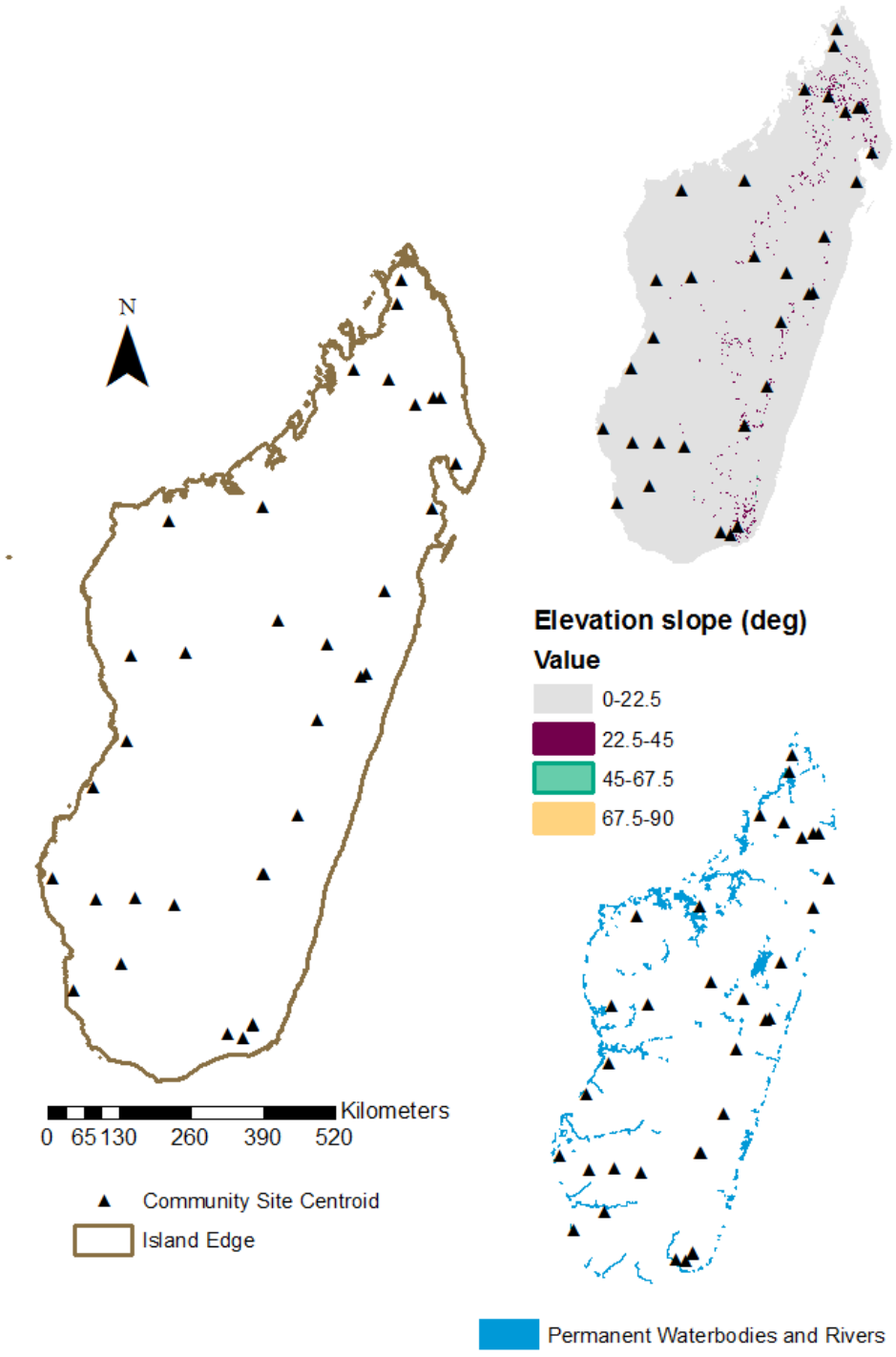


Figure 2.3. Biogeographic variables across Madagascar. Values are divided by natural breaks (Jenks) for visual clarity.

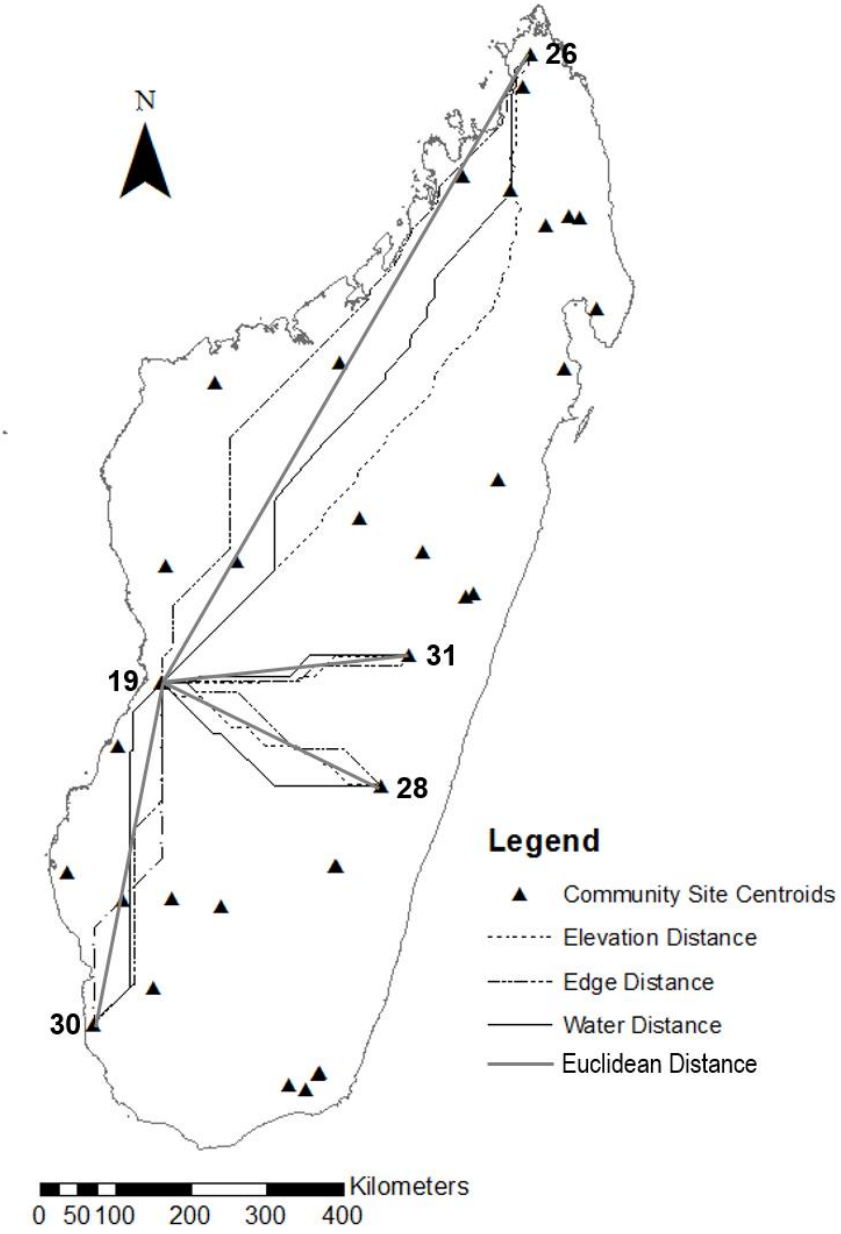


Figure 2.4. Biogeographic effective distances between site 19 and sites 26, 28, 30 and 31. The Euclidean (straight-line) distance is the shortest distance between sites, whereas the effective distances accounting for elevation slope changes, traveling within the island edge and around permanent water bodies and rivers are longer. Names of the numbered sites are in Table A.1.

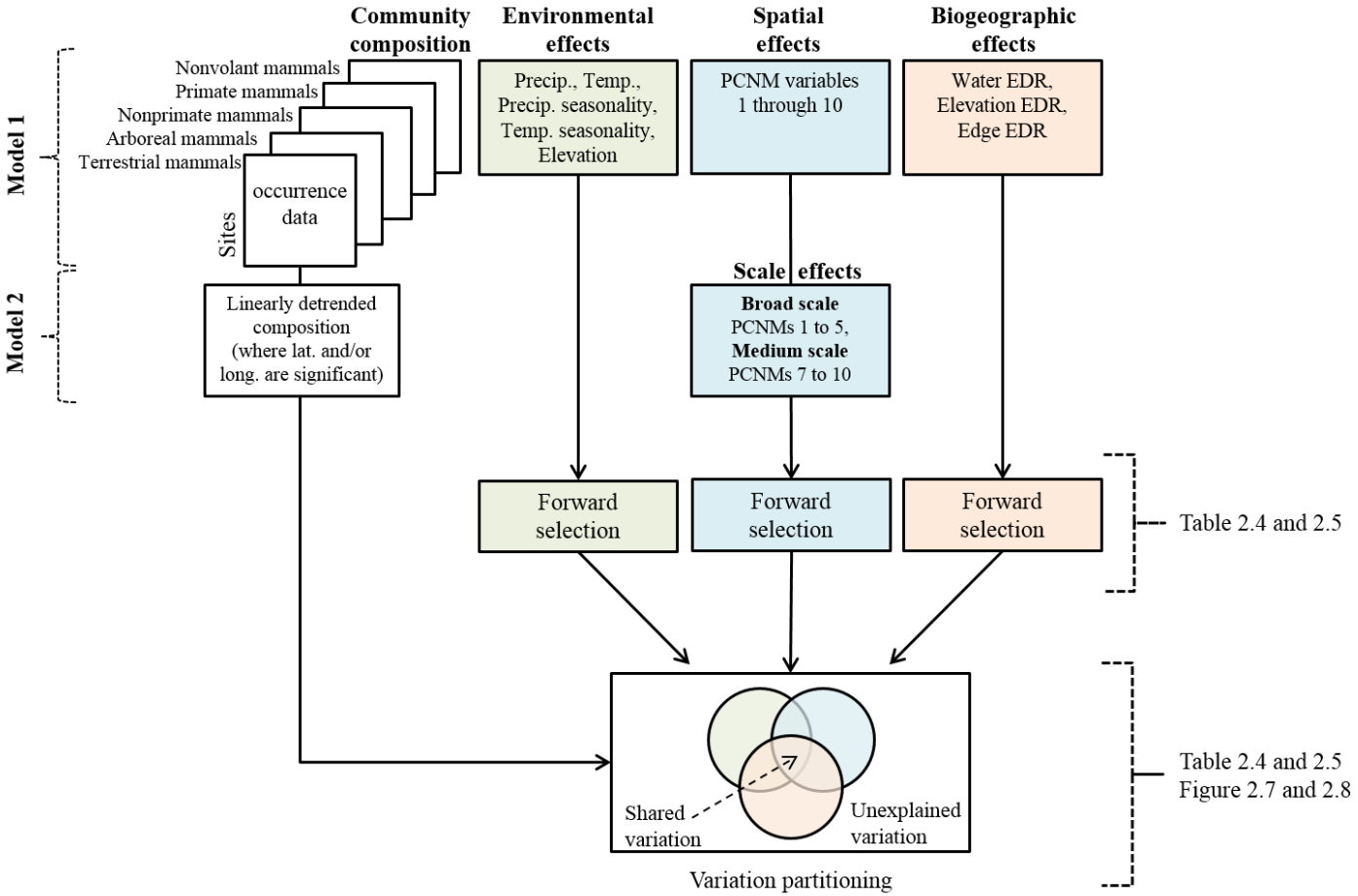


Figure 2.5. Schematic of the different datasets used and the analytical steps performed in this chapter to identify the community assembly processes shaping nonvolant mammal communities in Madagascar. Steps were repeated for each community type. Results of analyses are provided in indicated tables and figures. This schematic is based on Figure 1.6, the analytical framework for the dissertation. Abbreviations: lat., latitude; long., longitude; Precip., precipitation; Temp., temperature; PCNM, principal coordinates of neighbour matrices; EDR, effective distance ratio.

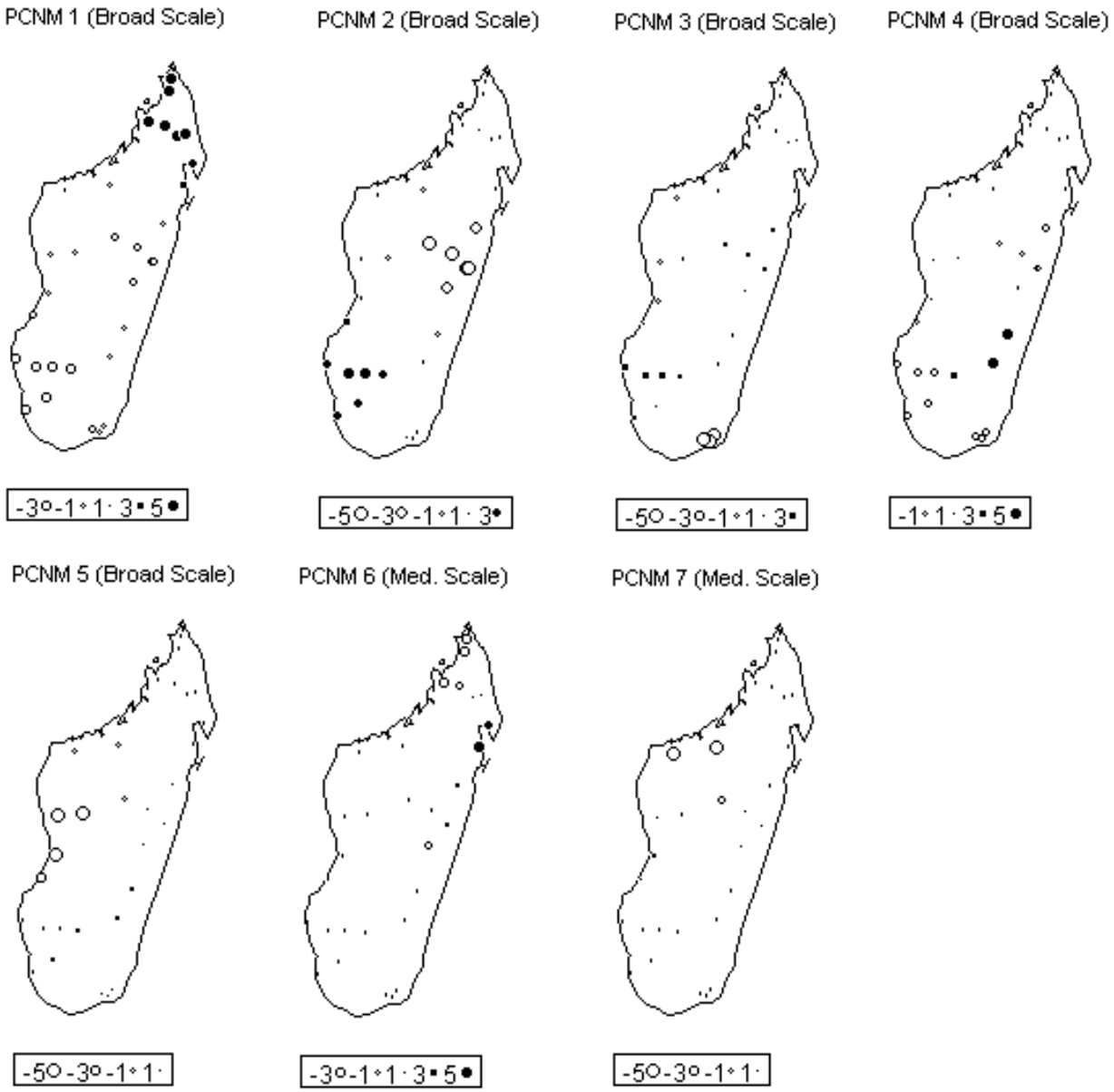


Figure 2.6. The significant forward selected Principal Coordinate of Neighbour Matrices (PCNM) variables with positive spatial correlation used in the PCNM analysis (shown on a map of Madagascar). PCNMs 1-5 depicted broad spatial scales and PCNMs 6 and 7 depicted medium (Med.) spatial scales. The circles of similar size and colour represent sites structured at similar spatial scales. Filled circles: positive eigenvalues; empty circles: negative eigenvalues.

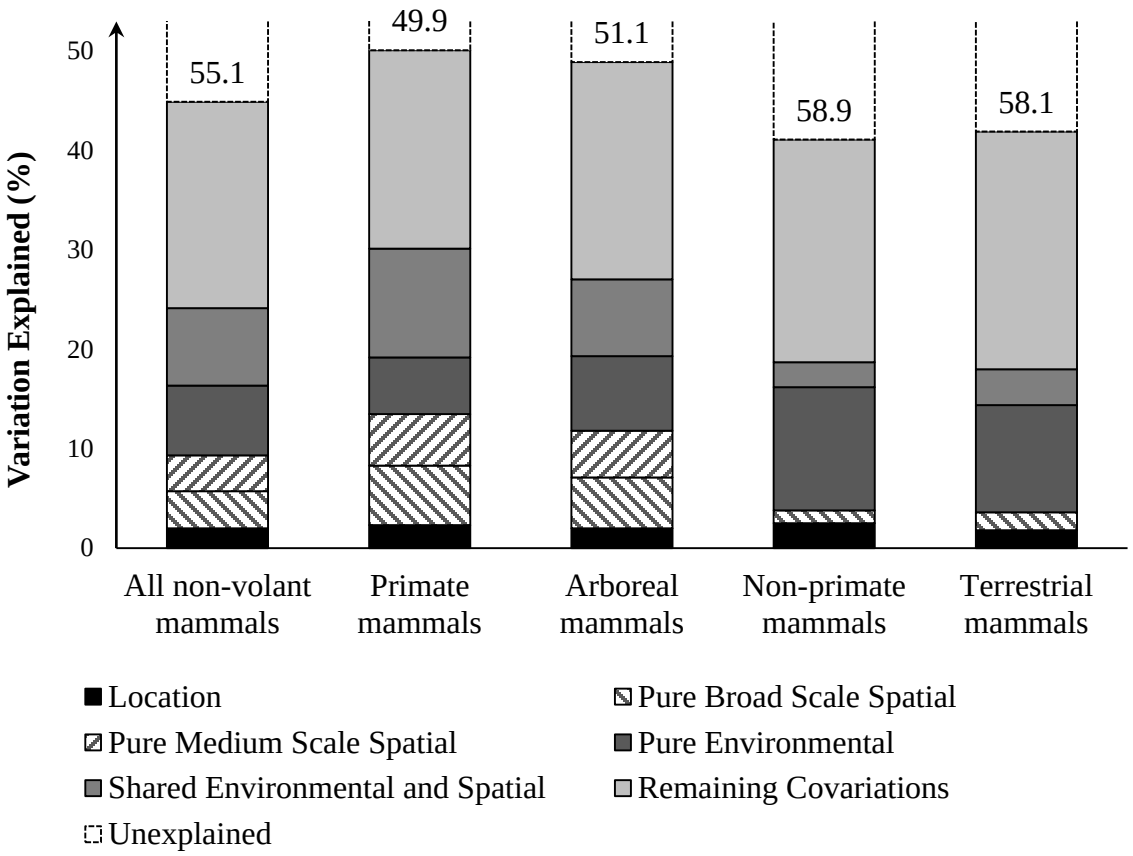


Figure 2.7. Percent of variation in nondetrended community composition explained by location, environmental, biogeographic, and spatial effects for 34 nonvolant, primate, arboreal, non-primate, and terrestrial mammal communities in Madagascar. For clarity, unexplained variation is a numeric value at the top of each column.

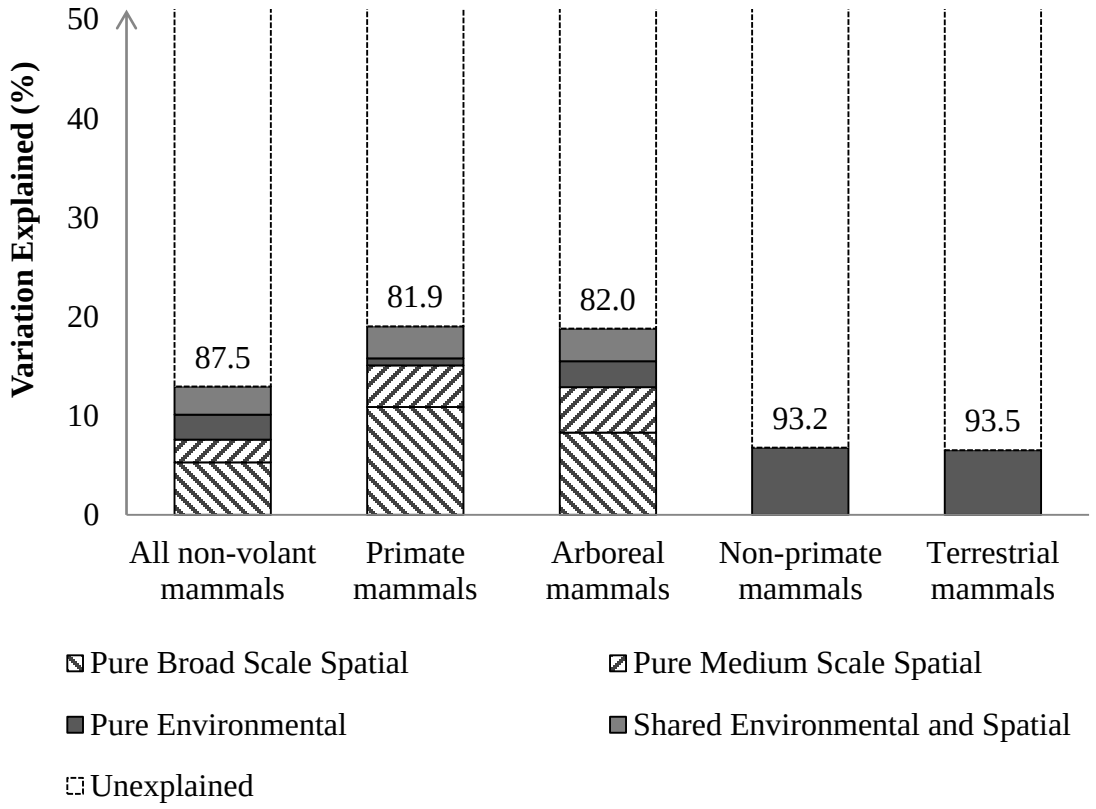


Figure 2.8. Percent of variation in detrended community composition explained by environmental and spatial effects for 34 nonvolant, primate, arboreal, non-primate, and terrestrial mammal communities in Madagascar. For clarity, unexplained variation is a numeric value at the top of each column.

Chapter 3: Taxonomic, functional and phylogenetic diversity measures tell different primate community assembly stories

INTRODUCTION

Primate communities have been the subject of an increasing number of research studies focused on identifying the assembly processes that have resulted in regional patterning of primate diversity (e.g., Beaudrot and Marshall 2011; Ganzhorn 1997; Gavilanez and Stevens 2013; Kamilar 2009; Muldoon and Goodman 2010). Deterministic and stochastic processes have been the predominant focus of these studies. Deterministic processes result in niche-based non-random patterns of diversity, resulting from environmental sorting and/or competitive interactions (Chase and Leibold 2003, Chase and Myers 2011). Stochastic processes describe patterns in diversity that are indistinguishable from random chance (Chase and Myers 2011), which can result from dispersal limitation and ecological drift (Hubbel 2001). However, a third set of processes, biogeographic processes, are also a potential contributor to the assembly of primate communities (e.g., Harcourt and Wood 2012; Vences et al. 2009; Gavilanez and Stevens 2013). Biogeographic processes include biogeographic dispersal barriers, resulting in differential survival and spread of populations (Tokeshi 1999), and preventing species from occupying all ecologically ideal habitats (Simpson 1953; Vences et al. 2009). Primate communities are a model taxon for testing the contribution of community assembly processes to patterns of diversity (e.g., Beaudrot and Marshall 2011; Cooper et al. 2008; Kamilar 2009; Kamilar and Guidi 2010) since comprehensive global data on community composition and species ranges of primates are better known than for any other vertebrate taxon (*sensu* Kamilar and Beaudrot 2013).

However, the predominant approach for identifying the relative contribution of each process to shaping ecological, and primate, communities is to examine taxonomic diversity, specifically species turnover (β-diversity) and to relate it to environmental and spatial distances between communities (e.g., Chalcraft et al. 2004; Korhonen et al. 2010; Legendre et al. 2005; Tuomisto and Ruokolainen 2006; Soinen et al. 2007). Communities are described with species lists of occurrence and/or abundance data (Tuomisto 2010a; 2010b; 2010c). Increasingly however, ecologists have used functionally- (e.g., Pakemen 2011; Siefert et al. 2013) and phylogenetically-based (e.g., Gomez et al. 2010; Gavilanez and Stevens 2013; Mason and Pavoine 2013) investigations of community richness and diversity as alternative measures (e.g., both: Pavoine and Bonsall 2011; Purschke et al. 2013; Spasojevic and Suding 2012). Functional diversity is a measure of functional trait diversity (Petchey and Gaston 2006). A functional trait is any morphological, physiological, or phenological trait that affects an organism's growth, reproduction, or survival and, ultimately, fitness (McGill et al. 2006; Petchey and Gaston 2006; Violle et al. 2007). Phylogenetic diversity describes the variance in evolutionary distances between species of a given community, and is computed from a phylogenetic tree based on a molecular phylogeny (Faith 1992). Functional and phylogenetic diversity are thought to reflect species niche similarity, depending on (1) the choice of traits, (2) the degree of phylogenetic signal in traits, and (3) the degree to which phylogenetic relatedness indicates functional relatedness (Thuiller et al. 2010; Sokol et al. 2011; Webb et al. 2002).

Including phylogenetic and functional trait information can help generate estimates of the relative differences in ecological roles among species (Devictor et al. 2010; Graham and Fine 2008; Graham et al. 2009; Scheckenbach et al. 2010; Swenson 2011), potentially providing greater insight into underlying assembly processes (McClain

et al. 2011). When niche-based environmental sorting, a deterministic process, operates species with shared ecological tolerances are found in areas with shared environmental attributes (Diaz and Cabido 2001; de Bello et al. 2005; Grime 2006). Consequently, a pattern of related species sharing similar ecological traits and preferences can result, creating a pattern of functional similarity (Cornwell et al. 2006; Grime 2006; Holdoway and Sparrow 2006) and phylogenetic clustering (Webb 2000; Table 3.2). Alternatively, competition between closely related taxa at local scales with similar resource requirements can prevent their co-occurrence and cause a pattern of phylogenetic overdispersion, in which species are less functionally (Holdoway and Sparrow 2006) and phylogenetically related than expected by chance (Webb et al. 2002). If stochastic (or neutral) processes are dominant, phylogenetic and functional community structure should exhibit a random pattern (Kembel and Hubbell 2006), or with dispersal limitation exhibit spatial clustering of phylogenetically similar individuals (Eiserhardt et al. 2013; Graham et al. 2009; Levine and Murrell 2003; Table 3.2). However, these phylogenetic predictions assume that resource-related traits are phylogenetically conserved, however, this assumption is not always appropriate (Losos 2008; Losos et al. 2003).

In Madagascar, phylogenetic similarity and ecological similarity are thought to be weakly correlated due to historical rapid adaptive radiations on the island (Kamilar and Guidi 2010; Kamilar and Muldoon 2010). In which case, convergence in traits may be more informative than taxonomic assemblages or phylogenetic diversity (Losos 2008), because the assumption that closely related species are ecologically similar is violated. Where a decoupling in phylogenetic and functional diversity exists, environmental sorting can result in patterns of phylogenetic overdispersion with distantly related species converging on similar ecological adaptations (Kraft et al. 2007). Consequently, the combined study of taxonomic, functional and phylogenetic diversity in community

assembly is critical to appropriately interpreting assembly patterns, and may also imply the operation of different community assembly processes (Cadotte et al. 2011; Cornwell et al. 2006; Mayfield et al. 2005; McGill et al. 2006; Spasojevic and Suding 2012; Stubbs and Wilson 2004; Weiher et al. 1998).

Madagascar's diverse and endemic primate communities are the result of the island's long isolation from other landmasses (from Africa ~ 120-130 Ma and from India ~80 Ma), and a large diversity of ecosystems and habitat types (including spiny deserts and montane humid rainforests) on a small geographic scale that are comparable with most continents (Goodman and Benstead 2005; Vences et al. 2009; Yoder and Nowak 2006). Madagascar is also characterized by climatic variability (Dewar and Richard 2007) and elevation changes (Yoder and Nowak 2006). This wide array of historical and environmental influences has resulted in high species diversification in lemurs (Vences et al. 2009; Yoder and Nowak 2006), represented by 5 families, 15 genera, and 99 endemic species (Mittermeier et al. 2008) with high trait diversity (Wright 1999). Madagascar's primates also differ from other primates in their evolutionary history. Lemurs underwent rapid diversification from a single common ancestor in the absence of mammal and avian species that compete with primates elsewhere (Karanth et al. 2005; Yoder and Yang 2004). The combination of Madagascar's history, environmental and endemic primate species richness makes it a particularly interesting site for the study of functional and phylogenetic primate community assembly.

However, the combined utility of taxonomic, functional and phylogenetic measures of diversity in detecting patterns of community assembly has not been evaluated in primates or mammals generally. Globally, the taxonomic (beta) diversity of primate communities is mostly driven by dispersal limitation (Beaudrot and Marshall 2011) consistent with the neutral theory of community assembly (Hubbell 2001), a

stochastic process. Phylogenetically, primate communities globally are randomly structured (Kamilar and Guidi 2010). However, in Madagascar, unique primate community assembly patterns exist. Both environmental and spatial variables, proxy measures of environmental sorting and dispersal limitation, shape the assembly of the taxonomic diversity of primate communities (Beaudrot and Marshall 2011; Muldoon and Goodman 2010; chapter 2), with dispersal limitation playing an arguably more important role (chapter 2). Although, functional groupings (e.g., terrestrial versus arboreal communities) have been shown to have contrasting community assembly patterns (chapter 2) and the functional diversity or trait types between Holocene and extant primate communities have been compared (Razafindratsima et al. 2013), their contribution to assembly has not yet been explicitly examined. Studies of phylogenetic diversity have suggested that Malagasy primate communities are phylogenetically overdispersed and have a weak correlation with phylogenetic diversity, which is probably due to roles of past competition and the recent extinction of numerous lemur species (Kamilar and Guidi 2010; Razafindratsima et al. 2013).

In this study, I test whether taxonomic, functional and phylogenetic measures of primate diversity in Madagascar are differentially shaped by community assembly processes in a spatially explicit manner. The objectives of this study are (1) to describe patterns of taxonomic, functional and phylogenetic diversity for extant Malagasy primate communities; and (2) to explore if and how taxonomic, functional, and phylogenetic measures of diversity are differently shaped by community assembly processes. Using 12 measures that encapsulate multiple facets of taxonomic, functional, and phylogenetic diversity (Table 3.1), I describe diversity patterns in 34 primate communities across Madagascar. In addition to investigating regional patterns in taxonomic, functional and phylogenetic diversity, I also partition the explained variation for each diversity measure

due to environmental variables (testing the contribution of environmental sorting), spatial variables (constructed with principal coordinates of neighbour matrices and testing the contribution of dispersal limitation), and biogeographic variables (measured with dispersal distance ratios; chapter 2). I test four major hypotheses based on regional diversity differences and the action of deterministic (environmental sorting), stochastic (dispersal limitation by distance) and biogeographic processes (biogeographic dispersal barriers; outlined below). Specific metric-level predictions are provided in Table 3.2.

Broad-scale community differences between eastern and western Madagascar have been previously described and posited to be due to bioclimatic differences between regions that may shape general patterns of diversity (e.g., Lees et al. 1999; Ganzhorn et al. 1999; Muldoon and Goodman 2010; Vences et al. 2009). Previous research has also shown primate taxonomic diversity patterns in Madagascar are generally characterized by ecoregional variation (Muldoon and Simons 2007; Muldoon and Goodman 2010), or broad-scale spatial structures (cf. chapter 2). Consequently, inherent to a study of the patterns of diversity present in Malagasy primate communities is an investigation of how patterns are geographically structured, i.e. by latitude and ecoregion.

Hypothesis 1: Patterns of diversity in Madagascar are geographically structured.

Prediction 1.1: Patterns of taxonomic, functional, and phylogenetic diversity are significantly different between eastern and western Madagascar.

Prediction 1.2: Patterns of taxonomic, functional, and phylogenetic diversity are significantly different between ecoregions.

Previous studies of the assembly of Malagasy primate communities using taxonomic measures of diversity (composition and β) showed that primate diversity is shaped by environmental sorting and dispersal limitation by distance (using

environmental and spatial variables; Kamilar 2009; Beaudrot and Marshall 2011; chapter 2), and dispersal around biogeographic barriers did not explain patterns of community composition (chapter 2). If environmental sorting has shaped patterns of primate taxonomic diversity then diversity values will correlate with environmental variables, and similar taxonomic diversity values will be present in environmentally similar sites; different taxonomic diversity values will be present in environmentally different sites (Chase 2003, 2007; Chase and Myers 2011). If dispersal limitation by distance has shaped patterns of primate taxonomic diversity then diversity values will correlate with geographic distance between sites. Values will be similar in sites that are geographically close and different in sites that are geographically far (Hubbel 2001; Loreau and Mouquet 1999; Mouquet and Loreau 2003).

Hypothesis 2: Primate taxonomic diversity is shaped by environmental sorting and dispersal limitation by distance.

Prediction 2.1: Patterns of taxonomic diversity correlate with both environmental variables and the distance between sites. Similar taxonomic diversity values are found in sites that are ecologically similar and geographically close together.

Prediction 2.2: Environmental (environmental effects) and spatial variables (spatial effects) explain the greatest proportions of variation in taxonomic diversity measures.

Previous work dividing primate communities into functional groups (e.g., Ganzhorn 1997; chapter 2) and investigating climatic niche space (Kamilar and Muldoon 2010) suggests that patterns of functional diversity may be variably influenced by assembly processes, depending on the traits tested. For example, Ganzhorn's (1997) study of Fox's assembly rules (each species entering a community will be drawn from a different group until each group is represented; Fox1987) in Madagascar classified diurnal lemur communities by dietary guilds and suggested that interspecific competition

shapes community and guild membership. Conversely, chapter 2 showed that spatial variables (modelling dispersal limitation) variably influence arboreal and terrestrial mammal communities in Madagascar. Overall, however, functional diversity is largely determined by environmental filtering (Grime 2006; Cornwell et al. 2006). In this study, I use a suite of traits that indicate various axes of resource use in primates (Table A.5). Consequently, patterns of functional diversity are expected to be strongly correlated with environmental conditions (Cornwell et al. 2006; de Bello et al. 2005; Diaz et al. 1998; Diaz and Cabido 2001; Grime 2006; Lessard et al. 2012). Primate species with shared ecological tolerances should be found in similar environments. Environmental sorting will have limited the range of viable traits, and resulted in decreased functional divergence/dispersion within similar environments and increased divergence/dispersion between different environments (Cornwell et al. 2006; de Bello et al. 2005; Diaz and Cabido 2001; Grime 2006; Holdoway and Sparrow 2006; Lessard et al. 2012; Siefert 2012; Weiher et al. 1998).

Hypothesis 3: Primate functional diversity is shaped by environmental sorting.

Prediction 3.1: Patterns of functional diversity correlate with environmental variables. Similar functional diversity values are found in sites that are ecologically similar.

Prediction 3.2: Environmental variables (environmental effects) explain the greatest proportions of variation in functional diversity measures.

Patterns of phylogenetic diversity may reflect niche-based processes (e.g., competition and habitat filtering), evolutionary/biogeographic processes (CavenderBares et al. 2009; Kembel 2009), and/or spatial processes through dispersal limitation (Eiserhardt et al. 2013; Graham et al. 2009). In Madagascar, primate communities are overdispersed and have significantly low NTI values (Kamilar and Guidi 2010), indicating that the most closely related species in communities are phylogenetically

distinct, and potentially a result of inter-specific competition, assuming biological traits are evolutionarily conserved (Kamilar and Guidi 2010; Kraft et al. 2007; Webb et al. 2002;). Patterns of species diversification in Madagascar are congruent with ecoregions (e.g., Boumans et al. 2007; Wilmé et al. 2006; Wilmé and Callmander 2006). However, phylogenetic diversity in Malagasy primates is weakly related to their climatic niches (Kamilar and Muldoon 2010). Patterns of diversity are geographically homogeneous where sites are bounded by the same biogeographic barriers, and heterogeneous due to past patterns of allopatric speciation or different species present between areas bounded by biogeographic barriers (Simpson 1953; Tokeshi 1999; Vences et al. 2009). In addition, monophyletic lineages that have undergone rapid adaptive radiation in a region, such as the lemurs of Madagascar, are expected to display functional and phylogenetic overdispersion (Cavender-Bares et al. 2006).

Hypothesis 4: Primate phylogenetic diversity is shaped by environmental sorting and biogeographic dispersal barriers.

Prediction 4.1: Patterns of phylogenetic diversity correlate with environmental variables and biogeographic variables. Similar phylogenetic diversity values are found in sites that are ecologically similar and have similar site isolation values.

Prediction 4.2: Environmental (environmental effects) and biogeographic variables (biogeographic effects) explain the greatest proportions of variation in phylogenetic diversity measures.

METHODS

Data Collection and Preparation

Data were collected for 34 protected areas in Madagascar (Figure 3.1). For each protected area the area in square kilometers encompassed by the protected area

boundaries was calculated from shapefiles (Table A.3), and the year protection began was collected from published sources (Table A.3). Primate community composition was assessed by compiling occurrence data for species from published sources of confirmed sighting data (Table A.1), following Mittermeier et al.'s (2010) taxonomy for primates. Taxonomic identifications were assigned to the species level. An ecological community was defined as all the nonvolant mammal species that potentially interact within a single patch or local area of habitat (Chase and Leibold 2003; Emerson and Gillespie 2008; Holyoak et al. 2005).

For each species, I obtained data on eight traits from the literature, including adult body mass, substrate type, feeding guild, trophic level, type of locomotion, activity period, habitat specificity, and presence of torpor (Table A.5). Traits were chosen to reflect ecologically relevant adaptations that relate to resource use and niche separation. Body mass is a key ecological trait, influencing a species' substrate use, resource requirements, competitive ability, population density and home range size (reviewed in Ganzhorn 1999). Substrate type (arboreal, terrestrial, both), feeding guild (frugivore, folivore, granivore, gumnivore, insectivore, carnivore and omnivore), and trophic level were chosen to describe the feeding resource requirements and niche separation of each species (e.g., Ganzhorn 1988; Gautier-Hion et al. 1980; McGraw and Bshary 2002). Trophic level was determined based on the assigned feeding guild. Locomotion is critical to travel, predator-avoidance, and foraging (Ripley 1967); types of locomotion included arboreal quadruped, vertical clinger and leaper, terrestrial quadruped, generalized quadruped (neither strictly arboreal nor terrestrial), fossorial and semi-aquatic. Activity pattern categories consisted of diurnal, nocturnal and cathemeral. I calculated habitat specificity as the number of ecoregions inhabited by each species based on their occurrence in each of the 34 communities. I chose this metric to differentiate between

species with widespread habitat distributions versus species with high habitat restriction. Finally, the presence of torpor in many Malagasy primate species, such as the Cheirogaleids (Schülke and Ostner 2007) reduces foraging requirements and exposure to predators, removing torpid species from the resource pool and mediating inter-specific competition (Geiser and Turbill 2009). Consequently, I view it as an important axis of niche differentiation in Malagasy primate communities.

Diversity Measures

Taxonomic diversity

Taxonomic diversity was measured in three ways (Table 3.1): α-diversity (species richness), community composition (species occurrence list), and β-diversity. Prior to analysis, community composition matrices (species x site) were Hellinger transformed to allow using RDA without considering the common absence of the species as a resemblance between communities (Legendre and Gallagher 2001). Additionally, prior to analysis a principal coordinates analysis (PCoA) with Lingoes correction for negative eigenvalues was used to describe the Jaccard dissimilarities between sites in two-dimensional space. The PCoA axes with eigenvalues of greater than one were retained for analysis, and are hereafter referred to as β-diversity. Taxonomic measures of diversity were calculated using the "vegan" (Oksanen et al. 2013) package in R.

Functional diversity

Functional diversity was measured with four diversity measures (FRic, FDiv, FDis, RaoQ; Table 3.1) that have been shown to effectively detect assembly processes for simulated communities under different assembly scenarios (*sensu* Laliberté and Legendre 2010; Mason et al. 2013; Mouchet et al. 2010). FRic and FDis are complementary measures of different components of functional variation that both need to be considered

in analysis (Mouchet et al. 2010; Laliberté and Legendre 2010). Dummy variables were assigned to categorical variables. Since the traits used to calculate measures of functional diversity consisted of both continuous and categorical variables, the Gower method was used to calculate distance matrices (for FDis) and all traits scores were standardized to have a range of 0–1 (Gower 1971; Laliberté and Legendre 2010; Laliberté and Shipley 2011). All functional diversity measures were calculated using the 'FD' package in [R] (Laliberté and Legendre 2010; Laliberté and Shipley 2011). The Cailliez correction to eliminate negative eigenvalues was used (Cailliez 1983; Laliberté and Legendre 2010).

Phylogenetic diversity

Phylogenetic diversity was calculated from a trimmed version of the primate consensus tree in the 10K Trees Project Version 3 (Arnold et al. 2010; Figure 3.2). The tree was trimmed using the Genbank taxonomy associated with the consensus tree to minimize the number of missing species (56 of the 70 species are present within this tree, with 7 species assigned to subspecies level of taxonomy, and one species assigned to a different genus; Table A.7). Five measures of phylogenetic diversity were used (Table 3.1): phylogenetic diversity (PDm), mean pairwise distance (MPD), mean nearest taxon distance (MNTD), nearest taxon index (NTI), and the net relatedness index (NRI). MPD, MNTD, NRI and NTI differ from PDm because they use a distance matrix as input rather than a phylogeny object. For NRI and NTI 1000 random assemblages were generated for the null models by selecting species only from within the set of taxa present in the community data (species pool) and shuffling the distance matrix across the taxa in the community (Kembel et al. 2010). Phylogenetic measures of diversity were calculated using the "ape" (Paradis et al. 2004) and "picante" (Kembel et al. 2010) packages in R.

Measures of diversity were statistically compared across eastern and western Madagascar and the main floristic regions (ecoregions). I used the WWF Terrestrial Ecoregions of the World classification schema (Olson et al. 2001; Figure 3.1). In this schema, habitats are assigned to two levels of classification: unique (country-level) ecoregions, and major habitat types (inter-regional and global). Unique ecoregions are habitat types that are particular to each country and are based on established country-level classification schemas. Major habitat types are broad (global) ecoregion classifications that group the unique ecoregions based on (1) comparable climatic regimes, (2) similar vegetation structure, (3) similar spatial patterns of biodiversity, (4) flora and fauna with similar guild structures and life histories, (5) similar minimum requirements and thresholds for maintaining certain biodiversity features, and (6) similar sensitivities to human disturbance (Olson and Dinerstein 2002). To maintain consistency with previous ecoregion assignments in Madagascar and to maximize sample sizes represented in each ecoregion study sites were assigned to the following four ecoregions: deserts and xeric shrublands (DES, n=10), subhumid forests (SHF, n=10), tropical and subtropical dry broadleaf forests (TSDBF, n=6), and lowland forests (LF, n=8). The DES ecoregion includes both the succulent woodlands and spiny thickets unique ecoregions. The TSDBF ecoregion is equivalent to the dry deciduous forests unique ecoregion. No primate communities were described for the mangroves or ericoid thickets unique ecoregions, which were therefore not included in this study's ecoregion classification. The east of Madagascar was classified as the region east of longitude 46.9º, which includes the SHF and LF ecoregions (Figure 3.1). The west of Madagascar is west of longitude 46.9º, including the DES and TSDBF ecoregions (Figure 3.1). Statistical differences between the east and west were determined with a two-sided t-test. Statistical differences across ecoregions were tested with an ANOVA.

Effect Types

Environmental effects

Georeferenced data on environmental variables for each study site were collected from the Madagascar Digital Elevation Model (CGIAR-SRTM data aggregated to 30s; Hijmans et al. 2004), and the WorldClim Global Climate Database (Hijmans et al. 2005; Table 2.2). I calculated mean values for each environmental variable within the protected area boundaries. Environmental variables were tested for significant autocorrelations (*sensu* Beaudrot and Marshall 2011) using Pearson's product-moment correlation coefficient. To minimize over-fitting models due to highly correlated environmental variables, I included variables in the analysis if they had a correlation of less than 0.8 and documented influences on mammal populations (Table 2.2).

Spatial effects

I used principal coordinates of neighbour matrices (PCNM) for the analysis of spatial effects across various spatial scales in the community composition data (Dray et al. 2006). The PCNM approach works well with presence/absence data and community data from multiple sites across space (Legendre et al. 2005). Furthermore, it can be used to detect significant correlations of community composition with environmental variables independent of spatial autocorrelation at a variety of spatial scales (Borcard and Legendre 2002; Borcard et al. 2004), which is important with geographically distributed data (Fortin and Dale 2005; González-Megías et al. 2005).

PCNM analysis creates spatial predictors that can be directly included in regression models by computing eigenfunctions of spatial connectivity matrices (Griffith and Peres-Neto 2006). PCNM uses a principal coordinate analysis of Euclidean distance matrix among study sites. The analysis truncates each matrix at the smallest distance

between nearest neighbours that keeps all sites connected in a single network (Figure 3.3). The eigenvectors (PCNMs) that modelled positive spatial correlation (Moran's I larger than expected value of Moran's I) were retained and used to represent spatial structuring in patterns of community composition. The first PCNMs represent broad scale spatial structures, with successive PCNMs representing progressively smaller spatial scale effects (Borcard and Legendre 2002), in this case ranging between 1400 km (broadest scale) to 26 km (smallest scale). Consequently, PCNMs with positive eigenvectors were evenly separated into small, medium and broad spatial scales to reflect the spatial grain of the study sites (*sensu* García et al. 2010). The use of the terms "small", "medium", and "broad" scales were defined relative to this particular set of study sites and were constrained by the data's resolution and spatial extent. PCNM variables were created using the R package ''PCNM'' (Legendre et al. 2010), based on geographic coordinates for each study site centroid. I calculated the geographic coordinates from the protected area boundaries (Gerber 2010) in ArcGIS 10.1 (Feature to Point tool) for each site.

Biogeographic effects

Biogeographic effects were measured as an effective distance ratio for each type of biogeographic barrier considered (permanent rivers and bodies of water, elevation slope, and the island edge; Figure 2.3). Data on the position of biogeographic dispersal barriers were extracted from digital maps of Madagascar, including permanent rivers and bodies of water, elevation slope, and the island edge (*sensu* chapter 2). Elevation slope was calculated from a digital elevation model of Madagascar using the Spatial Analyst extension in ArcGIS version 10.1, and divided into four equal categories of 22.5º increments (max of 90º). Least-cost paths (LCP) were calculated as measures of the

effective distance between each unique site pair based on the costs of crossing over or around biogeographic barriers (*sensu* chapter 2). Using the Spatial Analyst extension in ArcGIS version 10.1 (ESRI) and a custom Python script, I performed the LCP analysis in which the path resulting in the lowest cost to reach a target site from the origin site was identified (chapter 2). LCPs between sites were measured with a friction layer that depicted the cost of crossing a habitat with biogeographic barriers present. A simple model was used where a prohibitively high cost was assigned to permanent biogeographic barriers (permanent water bodies, permanent rivers, and the island edge) and remaining habitat had no cost assigned to it. The 0º to 45º slope increments were assigned the lowest travel cost, the 45 to 70.5º increment was assigned a moderate cost, and 70.5º to 90º the highest and most prohibitive cost. These divisions and assigned costs were chosen to reflect the energetic costs of travelling over terrains with higher travel costs (*sensu* Wade et al. 1998). This analysis was conducted separately for every unique site pair and each type of barrier (island edge, permanent water bodies and rivers, slope changes in elevation). Each biogeographic effective distance between site pairs was then divided by the Euclidean distance between sites, to account for the sole effect of biogeographic barriers as a biogeographic effective distance ratio. Biogeographic effective distance ratios for each origin site to every destination site were averaged for each origin site to serve as a measure of site isolation of each site relative to other sites (Equation 2.1).

Statistical Analyses

All analyses were conducted in R 3.1.0. I modeled the multivariate response of Madagascar's primate communities to a matrix of environmental variables, spatial variables (PCNMs) and biogeographic effective distance ratios using variation

partitioning techniques for 12 measures of diversity. In this modelling approach, diversity was the response variable, and the environmental, spatial and biogeographic variable sets were the explanatory variables (Figure 3.4).

Diversity Correlations

Linear and log-linear regressions were used to test the statistical relationships between diversity measures and species richness (α-diversity). Correlations between all measures of diversity were measured with Pearson correlation coefficients. Species-area relationships (SARs) were investigated to identify positive relationships between species richness and area (Rosenzweig 1995). I tested the relationship between alpha diversity and protected area size using a linear model, the log-log linear model (or power model), the non-linear Arrhenius model, and the Gleason model. These model types were tested to account for a potential non-linear relationship between alpha diversity and area, and these SAR models have been shown to fit data well (Tjørve 2003, 2009). SAR model fits were compared using the Aikake criterion (AIC), where a lower number represents better model fit (Aikake 1974). I also tested the relationship between alpha diversity and protected area age (year protected area gazetted subtracted from 2014) with a linear regression.

Principal Coordinates of Neighbour Matrices

Community composition data were checked for the presence of linear trends (trend between composition and geographic coordinates) using RDA and an ANOVA with 1000 permutations. A significant trend indicates the presence of spatial effects at broader scales than the sampling extent, or a gradient across the entire studied area (Borcard et al. 2004). Composition needs to be detrended for PCNM analysis, or a large number of PCNMs are necessary to model the linear trend in composition and their role

in modelling finer spatial scales might go unnoticed (Borcard et al. 2004). Thus, when the linear trend was significant, composition matrices were regressed against longitude and latitude and the residuals retained as response variables (detrended; *sensu* Borcard et al. 2004; Legendre and Legendre 2012). Both nondetrended and detrended (where applicable) composition matrices were retained for analysis because including the linear trend in composition (nondetrended) is equivalent to modelling the spatial pattern of composition at the broadest spatial scale (all of Madagascar), while detrending allows for modelling smaller spatial scales (detrended; Figure 3.4).

Global models (with complete sets of explanatory variables, Table 2.2) for each community grouping and effect type (location, environmental, spatial, biogeographic) were tested for significance with a RDA and an ANOVA with 1000 permutations, from which the global adjusted R^2 value was calculated. I then used a forward selection procedure (Figure 3.4) to retain the variables (latitude and longitude, PCNMs, environment, biogeographic; Table 2.2) with the highest explanatory power while preserving interactions between variables and producing the most parsimonious model (Legendre and Legendre 2012). In addition, the contribution of protected are features (size and age) were tested to account for their potential influences on community diversity. For each significant global model, I completed a forward selection with 9999 Monte Carlo permutation tests and used a double stopping criterion was where the selection stopped if either a p-value of 0.05 or the global adjusted R^2 were exceeded (Blanchet et al. 2008). I repeated the forward selection process for each variable group and each diversity measure individually. The RDA and tests of significance were computed with the "rda" and "anova.cca" functions of the "vegan" library in R (Oksanen et al. 2008), and the "forward.sel" function in the "packfor" package (Dray et al. 2011) was used for forward selection. (Figure 3.4)

Variation Partitioning

Variation partitioning was then used to identify the components of variation in community composition explained by location, environmental effects, spatial effects, and biogeographic barriers (e.g., Gilbert and Lechowicz 2004; Jones et al. 2008; Kamilar 2009; Legendre et al. 2005; Lindo and Winchester 2009). Variation partitioning was carried out using the "varpart" function of the "vegan" R package (Oksanen et al. 2008), which uses RDA to compute the variation attributable to each set of explanatory variables. I used the adjusted R^2 statistic to assess the proportion of the response variation explained by each explanatory data set and their combinations. The adjusted R^2 provides unbiased estimates of the explained variation (Peres-Neto et al. 2006). Only variables selected in the forward selection procedure were included in the variation partitioning analyses. I used partial RDAs and ANOVAs to test the significance of each pure component of variation while controlling for other variable sets. For example, I tested the significance of the amount of variation due to environmental effects for significance while controlling for spatial and biogeographic effects. When variation was shared between PCNMs and other components of variation (environmental variables and biogeographic effective distance ratios), that component of shared variation was interpreted as spatially structured (*sensu* Laliberté et al. 2009). Dividing the PCNMs into broad, medium, and small spatial scales showed the amount of variation attributed to those spatial scales. I did not test the proportion of variation due to protected area variables because they are not measures of the contribution of assembly processes to shaping community diversity.

I executed the variation partitioning analysis in two ways: (1) Model 1: using forward selected environmental, scale-specific PCNMs, and biogeographic variables and including the linear trend of composition and geographic location without detrending

composition (*sensu* Borcard et al. 2011); and (2) Model 2: using forward selected environmental, scale-specific PCNMs, and biogeographic variables with detrended community compositions (when latitude and/or longitude were significant). Several components of variation are reported: pure effects where the variation was attributable to a single source (e.g., pure environmental effects), total effects where the total amount of variation is attributable to a source and its covariations with other variables (e.g., total environmental effects), and shared spatial-environmental effects (the shared variation of environmental and spatial effects). Statistical tests were considered significant at $p < 0.05$.

RESULTS

Diversity Patterns across Madagascar

Patterns of primate diversity in Madagascar were varied, geographically distinct, and somewhat correlated (Table 3.3 and 3.4, Figures 3.5 to 3.7). Taxonomic diversity measures (α, composition and β) were different between eastern and western Madagascar and across ecoregions. Alpha diversity (species richness) ranged from 3-13 primate species per site, and showed significant differences between eastern and western Madagascar (t = 3.966, df = 31.994, p <0.001, Figure 3.6), and between ecoregions (F(3,30) = 5.341, p = 0.004, Figure 3.6), with higher α-diversity in eastern sites (SHF, LF; $\bar{x}$ = 10.17) versus the western sites ($\bar{x}$ = 7.19). The primate species occurrence list across all 34 sites comprised 70 species, representing five families and 15 genera. Composition was distinct between the DES and TSDBF dry ecoregions characterizing the west, and similar between the SHF and LF humid ecoregions characterizing the east, where high overlap in species composition hulls was high (Figure 3.5). Site 21 (Monangarivo) groups closer to the TSDBF ecoregion group than with the LF ecoregion group. Monangarivo is on the northwestern side of the island, in contrast to the majority

of LF sites. Monangarivo is isolated from the other LF sites by a section of SHF and borders the TSDBF ecoregion, contributing to its high similarity with TSDBF primate communities. The first PCoA axis of the Jaccard index (β-diversity) also showed significant differences between east and west Madagascar (t = 10.275, df = 22.898, p < 0.001) and across ecoregions (F(3,30) = 109.12, p < 0.001), indicating dissimilar species composition between regions in Madagascar.

Across functional diversity measures, functional diversity was higher in the west than the east, encompassing more diverse traits and higher trait variation, particularly in the TSDBF and DES ecoregions. Functional diversity measured as functional richness was significantly different between the eastern and western regions of Madagascar (FRic; t = -3.567, df = 22.69, p = 0.002), and not signification for functional divergence (FDiv; t = -1.046, df = 21.79, p = 0.307; Figure 3.6). The range of values for both measures in the east (FRic: 0.527-0.752, FDiv: 0.729-0.846) were encompassed by the range of values observed in the west (FRic: 0.544-0.951, FDiv: 0.723-0.939). Between ecoregions, however, significant differences existed for FRic (F(3,30) = 6.758, p = 0.001), where DES has the highest overall functional richness, and not for FDiv (Figure 3.7). Functional dispersion (FDis; t = -4.976, df = 18.489, p < 0.001) and Rao's quadratic entropy (RaoQ; t = -4.906, df = 17.629, p < 0.001) were both significantly different between eastern and western Madagascar with lower values observed in the east. Across ecoregions, FDis (F(3,30) = 9.854, p < 0.001) and RaoQ (F(3,30) = 11.777, p < 0.001) were significantly different with the highest values observed in the DES ecoregion and the lowest in the humid ecoregions (SHF and LF).

Phylogenetic measures of diversity were significantly different between eastern and western Madagascar for PDm (t = 2.894, df = 29.969, p = 0.007) and NTI (t = -2.168, df = 26.35, p = 0.039, Figure 3.6), and across ecoregions for PDm (F(3,30) = 3.853, p =

0.019) and NRI ($F(3,30) = 3.750$, $p = 0.021$; Figure 3.7). The relative phylogenetic age of primate communities was older in the east than the west. No values of NTI or NRI were significantly different from zero over the 1000 simulations, indicating phylogenetic structuring of communities that were not significantly different from random. The mean p-value ± standard deviation for the comparison of observed NRI versus simulated NRI values was 0.836±0.127, and 0.898±0.169 for NTI. The lack of a significant difference between these values and the null expectations, and the prevalence of values close to zero suggests that most communities are comprised of a phylogenetically random set of species. Although these measures did not differ significantly from zero they can still be compared to each other and across ecoregions because their comparative values indicate the degree of clustering or overdispersion relative to each other (cf. Kamilar et al. 2014; Table 3.1). Consequently, the higher negative values of NRI ($\overline{x} = -1.259$) and NTI ($\overline{x} = -2.155$) in the east indicate respectively more phylogenetic clustering and low co-occurrence of closely related taxa than are observed in the west (east: $\overline{x} = -1.018$, west: $\overline{x} = -1.470$).

In general correlations between all pairs of diversity measures were not very strong ($r < |0.80|$), with the exception of FDis x RaoQ, α x PDm, MPD x NRI, and PDm x NTI (Figure 3.8). While a strong positive linear relationship existed between species richness (α) and PDm (Adj.$R^2 = 0.889$; Table 3.3), the other measures of diversity were not strongly related to α-diversity (Adj.$R^2 < 0.564$; Table 3.3, Figure 3.8). Correlations in diversity measures grouped by ecoregion, with clear demarcations present in β-diversity correlations. Subhumid forest sites and lowland forest sites, characterizing eastern Madagascar had values that highly overlapped, particularly for nonphylogenetic diversity correlations (Figure 3.8). Alpha diversity in Malagasy primate communities was not

significantly related to either the size of the protected area (regardless of model tested), nor the age of the protected area (Table 3.4).

Linear Trends in Diversity and Forward Selection of Variables

Global RDA models testing the contribution of latitude and longitude to observed patterns in diversity were significant for α-diversity ($F = 4.302$, $p = 0.025$), composition ($F = 6.437$, $p < 0.001$), β ($F = 38.533$, $p < 0.001$), FRic ($F = 5.621$, $p = 0.004$), FDis ($F = 9.002$, $p = 0.001$), RaoQ ($F = 11.287$, $p < 0.001$), and NRI ($F = 4.409$, $p = 0.008$; Table 3.5). Longitude was a significant variable in all three measures of taxonomic diversity, and for FRic, FDis and RaoQ. NRI was significantly shaped by Latitude. Global environmental models (climatic variables) were significant for α-diversity ($F = 4.365$, $p = 0.008$), composition ($F = 4.146$, $p < 0.001$), β ($F = 35.918$, $p < 0.001$), FRic ($F = 3.550$, $p = 0.004$), FDis ($F = 8.115$, $p < 0.001$), RaoQ ($F = 9.424$, $p < 0.001$), PDm ($F = 3.253$, $p = 0.019$), MPD ($F = 3.185$, $p = 0.029$), and NRI ($F = 3.682$, $p = 0.009$; Table 3.5). Annual precipitation was significant and for all three measures of taxonomic diversity and precipitation seasonality was significant for three of the four measures of functional diversity (FDis, FRic, and RaoQ). Of the measures of phylogenetic diversity, MPD and NRI were significantly shaped by elevation and annual temperature, whereas PDm was significantly shaped by annual precipitation. Protected area variables (size and age) were not significant forward selected variables for any measures of primate community diversity (Table 3.5).

Twenty-two PCNMs described the spatial connectedness of the 34 sites in Madagascar, of which 10 eigenvectors had positive spatial correlations. These 10 eigenvectors represented two spatial scales: broad (PCNMs 1-5) and medium (PCNMs 6-10) (Figure 3.9). No small-scale spatial structures were positive and/or significant

(PCNMs 10-20). PCNM 1 describes a latitudinal gradient between sites, differentiating the north from the south, and PCNM 2 describes a combination of a latitudinal and longitudinal division between primate communities in the northeast and those in the southwest (Figure 3.9). With decreasing spatial scales the patterns in site scores for each PCNM vector are more variable intra-regionally, with fewer apparent broad scale differences (across for example latitudinal or longitudinal lines, Figure 3.9). Significant global models of spatial variables (PCNMs) were significant for α ($F = 4.692$, $p = 0.003$), composition ($F = 3.528$, $p < 0.001$), β (F = 20.149, $p < 0.001$), FDis ($F = 5.322$, $p = 0.001$), RaoQ ($F = 6.109$, $p = 0.003$), PDm ($F = 2.797$, $p = 0.015$), and MPD ($F = 2.513$, $p = 0.031$; Table 3.5). Measures of α-diversity and composition had significant PCNMs at both broad and medium spatial scales, and β-diversity had spatial structures only at broad spatial scales. FDis and RaoQ were shaped by PCNMs at both broad and medium spatial scales. Phylogenetic diversity was poorly predicted by spatial variables, and of the two measures with significant spatial structures (PDm and MPD), only PDm had both broad and medium spatial variables forward selected. Biogeographic global models were only significant for composition ($F = 1.726$, $p = 0.005$), for which only the edge distance ratio was forward selected (Adj. $R^2 = 0.048$, $F = 2.659$, $p = 0.033$).

When diversity was detrended, global models including only biogeographic variables were not significant for any measure (Table 3.6). Environmental global models were significant for detrended composition ($F = 1.541$, $p = 0.006$), β-diversity ($F = 7.394$, $p < 0.001$), FDis ($F = 3.969$, $p = 0.007$), and RaoQ ($F = 3.775$, $p = 0.013$; Table 3.6). Spatial variables were significant for α-diversity ($F = 3.229$, $p = 0.013$; broad and medium), composition ($F = 1.818$, $p < 0.001$; broad and medium), β-diversity ($F = 3.345$, $p = 0.007$; broad), and FDis ($F = 2.545$, $p = 0.027$; broad and medium). Significant spatial structures were not present in detrended measures of phylogenetic diversity.

Variation Partitioning of Diversity Measures

Model 1

Explained variation in diversity measures was mostly attributed to location, environmental, and spatial variables (Table 3.7 and 3.8, Figure 3.10). The largest percent of variation explained in α-diversity was due to pure spatial effects (28.3%; Table 3.7), with medium-scale effects explaining more variation than broad scale effects (18.3% versus 11.5%; Table 3.8). Location and environmental variables explained small and non-significant proportions of variation although their total effects (including their covariations) were high (19.2% and 27.9%, respectively). Of the variation in β-diversity, 5.4% of the variation was significantly attributable to environmental variables, and 2.7% to spatial variables. Overwhelmingly the variation in β-diversity was explained by covariations between location, environmental and spatial variables (Table 3.7). Furthermore, the best fitting model of all twelve diversity measures was provided by β-diversity, with only 11.1% of the variation left unexplained. Composition, as reported in chapter 2, was significantly shaped by location (2.4%), environmental (5.3%) and spatial effects (8.6%). Furthermore, both broad and medium scale spatial structures were significant components of variation in composition (6.6% and 4.0%; Table 3.8). Overall, measures of taxonomic diversity were shaped by both spatial and environmental effects, with large portions of variation explained by covariations between location, environmental effects and spatial effects.

Of the functional diversity measures, FRic and FDis were significantly shaped by only one effect type, environment (13.2%, Table 3.7) and medium scale spatial effects (18.7%, Table 3.8), respectively (Figure 3.10). FDiv had no significant forward selected variables and was not tested with the variation partitioning approach. 8.6% of the variation in RaoQ was significantly explained by environmental effects, and 20.9%

explained by medium-scale spatial effects (Table 3.8, Figure 3.10). The best fitting functional diversity model was for RaoQ, with 70.5% of diversity explained in comparison to the weakest model for FRic, with 37.3% of the variation explained. Overall, functional diversity models were shaped by environmental effects and medium-scale spatial effects.

Phylogenetic diversity was poorly predicted by location, environmental and spatial effects (Table 3.7 and 3.8; Figure 3.10). Of the five phylogenetic diversity measures, MNTD and NTI had no fitted models due to no forward selected variables. Of the remaining measures, PDm had 10.3% of its variation significantly explained by spatial effects, and NRI had 13.5% of its variation significantly explained by environmental effects. MPD had no significant components of variation explained, and the majority of explained variation was due to a covariation between location and environment (32.9%). Of PDm, MPD and NRI, MPD had the best fitting model with 32.8% of variation explained despite the lack of significant pure effect types. PDm had the weakest fitting model with 27.8% of variation explained. Overall, phylogenetic diversity measures were variably shaped by environmental and spatial effects, and were poorly fit.

Model 2

Taxonomic diversity, once detrended, was shaped predominantly by spatial effects (Table 3.9, Figure 3.10). Detrended α-diversity had large components of variation significantly explained by broad (18.3%) and medium scale (21.9%) spatial effects. Beta diversity, once detrended, was only significantly explained by broad-scale spatial effects (15.4%). Both broad (10.8%) and medium (4.1%) scale spatial effects significantly explained composition. Again, β-diversity had the highest model fits with 52.9% of the

variation explained. FRic had no significant forward selected variables once detrended and was not tested with variation partitioning. Both FDis and RaoQ were significantly explained by environmental (FDis= 13.2%; RaoQ= 10.0%) and broad (FDis= 6.5%; RaoQ = 5.7%) and medium (FDis= 20.0%; RaoQ = 17.6%) scale spatial effects once detrended. NRI, the only detrended measure of phylogenetic diversity, had no forward selected variables, and therefore variation was not partitioned (Table 3.9, Figure 3.11). Overall, once the effect of location was removed (detrending), diversity patterns were due to a combination of environmental, broad and medium scale spatial effects. Environmental variables were strongly correlated with broad scale structures, explaining between 3.2 and 26.9% of the variation in detrended diversity (Table 3.9).

DISCUSSION

I found diversity metrics (depicted by different measures of taxonomic, functional and phylogenetic diversity) are indicative of the varying ways diversity is influenced by environmental, spatial, and biogeographic variables. While no ubiquitous combination of assembly processes contributed to the taxonomic, functional, or phylogenetic structuring of primate communities in Madagascar, the combined importance of both environmental sorting and dispersal limitation shaping primate communities was supported. As predicted, patterns of primate community diversity in Madagascar were strongly geographically structured with significant differences present in taxonomic, functional, and phylogenetic diversity between eastern and western Madagascar and across ecoregions. Overall, a combination of environmental and spatial effects shaped taxonomic measures of diversity, suggesting that environmental sorting and dispersal limitation by distance shape patterns of primate community taxonomic diversity. Functional diversity inconsistently followed predicted patterns. Environmental effects,

indicating the operation of environmental sorting, explained only one measure of functional diversity (FRic). The two measures of functional dispersion (FDis and RaoQ) were explained instead by a combination of environmental and spatial effects, with greater components of variation explained by pure spatial effects and covariations between variables, indicating the combined operation of environmental sorting and dispersal limitation by distance. The predicted community assembly patterns for phylogenetic diversity however had mixed support; two of the five measures were not explained by any assembly process and environmental and spatial effects differently explained the remaining three measures, with large proportions of variation due to covariations between environmental and spatial variables.

Two main factors probably contributed to the assembly differences between diversity measures: (1) different types of diversity (i.e. taxonomic, functional, phylogenetic) were fundamentally shaped by different combinations of assembly processes, and (2) different facets of each type of diversity (depicted by different measures of taxonomic, functional and phylogenetic diversity) were indicative of the varying ways diversity can be and are influenced by environmental, spatial, and biogeographic variables. Furthermore, for many diversity measures (composition, β, FDis, RaoQ, PDm, MPD, and NRI) the contribution of environmental and spatial factors was not fully separated because they were explained by covariations between location, environmental, and spatial effects in addition to the unique contributions of environmental and spatial effects to diversity patterns.

Primate Diversity Patterns in Madagascar

Taxonomic, functional and phylogenetic diversity were variably patterned and geographically dependent. The geographic dependence of the diversity measures was

indicated by three results: (1) α, β , FRic, FDis, RaoQ, PDm and NTI were significantly different between eastern and western Madagascar, (2) taxonomic (α, β), functional (FRic, FDis, RaoQ), and phylogenetic (PDm and NRI) diversity were significantly different across ecoregions, and (3) latitude and/or longitude were significant forward selected variables for seven of the twelve diversity measures (α, composition, β, FRic, FDis, RaoQ, and NRI). These diversity trends provide further evidence that ecoregional differences in Madagascar help shape patterns of diversity, taxonomic or otherwise (e.g., Muldoon and Simons 2007; Muldoon and Goodman 2010; chapter 2).

Madagascar's primate diversity was distinct between the east and the west, and coincided with ecoregional differences between the humid east (lowland forest sand subhumid forests) and the drier west (tropical and subtropical dry broadleaf forests, deserts and xeric shrublands). Higher overall species richness existed in the eastern regions of Madagascar, with the highest in the lowland forest ecoregion, and the lowest in the deserts and xeric shrubland ecoregion of southwest Madagascar. In addition, the composition of the subhumid forest and lowland forest sites were the most similar in contrast to the tropical and subtropical dry broadleaf forests and deserts and xeric shrubland ecoregions. Functional richness was also different, with higher functional diversity values observed in the west, and more clustered trait structures in the humid east. Furthermore, the primate communities in the western ecoregions (deserts and xeric shrublands and tropical and subtropical dry broadleaf forests) were characterized by larger ranges of functional diversity values than the east.

The differences in primate community diversity along latitudinal and ecoregional lines found in this study coincide with bioclimatic differences (e.g., Lees et al. 1999; Ganzhorn et al. 1999; Vences et al. 2009; Muldoon and Goodman 2010) driven by precipitation and temperature differences between the humid east and hotter and drier

west (Jury 2003). The east of Madagascar is typically associated with highly productive environments due to higher precipitation and lower precipitation seasonality than the west (e.g., Lahann et al. 2006). By contrast, the west is characterized by decreased precipitation compared to the east (e.g., Scholz and Kappeler 2004; Sorg and Rohner 1996), and unusually high interannual variation in precipitation (Dewar and Richard 2007). However, the east was also characterized by high environmental stochasticity (Dewar and Richard 2007; Donque 1975; Ganzhorn 1995) and by irregular and asynchronous fruiting schedules (Hemingway 1995; Morland 1993; Overdorff 1993; Powzyk 1997). The two ecoregions present in the east (SHF and LF) are environmentally more similar to each other than the two ecoregions characterizing the west (DES and TSDBF). Furthermore, the western sites include transitional zones between humid and dry habitats. For example Kirindy Mitea in the DES ecoregion is the largest continuous tract of dry deciduous forest in the world (Whitehurst et al. 2009) and serves as a transitional zone between the western dry forest and the southern spiny forest (Burgess et al. 2004; Moat and Smith 2007). Analalavelona, also in the DES ecoregion is significantly more humid than any other area in southwest Madagascar (Moat and Smith 2007). The variation present in western Madagascar has resulted in taxonomic assemblages that cluster well with each other (Figure 3.5) and yet has large ranges in trait structures that indicate a diverse suite of adaptations to diverse environments.

Community-level patterns of functional trait convergence, small trait space, occur when abiotic conditions determine establishment success, i.e., filter species according to their functional traits resulting in patterns of environmental sorting (e.g., Holdaway and Sparrow 2006; McGill et al. 2006; Weiher et al. 1998). Furthermore, functional dispersion (*sensu* functional divergence) may be a proxy measure for niche differentiation present in a community (Mason et al. 2005) and provides a good proxy

measure for ecosystem multifunctionality (Mouillot et al. 2011). I used two related measures of functional dispersion, FDis and RaoQ (Table 3.1; Laliberté and Legendre 2010). Although RaoQ is a combined measure of both functional divergence and functional richness (Díaz et al. 2007; Scherer-Lorenzen et al. 2007; Weigelt et al. 2008), both measures quantify the amount of dispersion of species in trait space while considering their relative abundances (in this case occurrence). In this study the low dispersion values (FDis and RaoQ) observed in the east compared to the west indicate a convergence in trait structure on particular habitat types. Where patterns in functional dispersion (FDis and RaoQ) contrast with functional divergence (i.e. functional dispersion is higher), functional differences are suggested to be due to a few highly distinctive species attributes (Villéger et al. 2008). In Malagasy primate communities, functional divergence was higher in the west, but not statistically different from the east, nor was it statistically significant across ecoregions. Across ecoregions the highest functional divergence values were in the TSDBF, indicating contrasting patterns within the west only. Malagasy primate communities have higher niche differentiation in the west than the east, and distinctive species attributes are prevalent in the TSDBF ecoregion. Montagne d'Ambre (site 26) the most northern site in this study and in the TSDBF ecoregion is unique, in that it has functional diversity values more similar to the humid ecoregions than to the other sites in the TSDBF ecoregion. Muldoon and Goodman (2010) in a study of nonvolant mammals also found that Montagne d'Ambre grouped better with northern humid ecoregion sites of transitional habitats than with sites in its own ecoregion. The diversity difference is likely due to mixed vegetation at Montagne d'Ambre with characteristics of both subhumid forest and dry deciduous western forest (Goodman et al. 1996).

Functional diversity is highly dependent upon the traits used in its calculation (Cornelissen et al. 2003; Mouchet et al. 2010). Some of the traits used in this study are documented to be geographically dependent (Albrecht et al. 1990; Muldoon and Goodman 2010; Muldoon and Simons 2007). Body mass of Malagasy primates is correlated with ecoregion, where ecoregions with low rainfall and long dry seasons (TSDBF, DES) have populations of smaller body sizes (Albrecht et al. 1990; Muldoon and Simons 2007). These patterns of body size with ecoregion may be due to climatic differences (e.g., rainfall: Gordon et al. 2013; Lehman et al. 2005; Lehman et al. 2007; but see Kamilar et al. 2012), resource differences (e.g., Ganzhorn et al. 1999; Lehman et al. 2005; Lehman 2007; Muldoon and Simons 2007; Ravosa et al. 1993), both or some other unmeasured variable. Furthermore, the relative percentages of omnivory, arboreal quadrupedalism, terrestrial/arboreal quadrupedalism and two body mass classes have been found to explain the majority of variation in the ecological structure of nonvolant mammal communities, which corresponded with ecoregions (Muldoon and Goodman 2010). Although functional traits reflect adaptations to different environments, environmental sorting acts upon whole individuals and therefore a suite of multiple traits (Grime 2002; Westoby et al. 2002). Traits such as torpor, an adaptation for energy conservation (Wright 1999) reducing foraging requirements and exposure to predators (Geiser and Turbill 2009; Schülke and Ostner 2007), accompanied small body size in this study. Species who use torpor (11 species in *Allocebus, Cheirogaleus* and *Microcebus*) had a mean body mass of 103g in comparison to 1904.84g for non-torpor species. They were predominantly omnivorous, were all nocturnal and varied in their distribution island-wide occupying between one and four ecoregions (Table A.6). Gumnivores were also infrequent (*Phaner* species) but accompanied by small body size and a nocturnal activity period. Furthermore, *Lemur catta* was the only terrestrial and arboreal primate

was classified as a generalized quadruped and occurred in all four ecoregions (Table A.6). The relative distribution of these species with these individual traits therefore has an influence on functional diversity measures, with rare traits increasing the hull volume and divergence values. Functional dispersion (FRic and RaoQ) values are somewhat insulated from these individual trait variations however because the relative frequency of trait values in a community is incorporated in the metric (Figure 1.5). Interspecific correlations between traits reflect the action of natural selection that facilitate the existence of certain trait combinations (Westoby et al. 2002), which in this study appear to be along environmental lines.

In contrast to taxonomic and functional diversity, primate phylogenetic diversity was not highly regionally variable. Phylogenetic diversity (PDm) was higher in the east than the west, and lower levels of related taxa co-occurring (measured as NTI) in the east versus the west of Madagascar. Despite previous research demonstrating species diversification processes in Madagascar that are congruent with ecoregions (e.g., Boumans et al. 2007; Wilmé et al. 2006; Wilmé and Callmander 2006), overall phylogenetic diversity was not different between ecoregions (except for PDm and NRI). However, Kamilar and Muldoon (2010) investigated functional convergence through climatic niches and phylogenetic diversity in Malagasy primates and found that closely related species had divergent climatic niches. They concluded that a phylogenetic signal is not a necessary outcome of diversification, and that climatic diversity is critical to patterns of primate diversity in Madagascar. Those results are congruent with this study, where patterns of functional diversity were ecoregionally variable, but phylogenetic patterns of diversity were not.

Diversity and Community Assembly

Taxonomic Diversity

Malagasy primate community assembly, using taxonomic diversity metrics, was previously shown to sort more strongly with environmental variables than spatial variables (Beaudrot and Marshall 2011; Kamilar 2009; Muldoon and Goodman 2010). In this study, however, both environmental (environmental sorting) and spatial effects (dispersal limitation by distance) shaped primate community taxonomic diversity, consistent with expectations and the results of chapter 2. Species richness (α) was spatially structured, with medium spatial scales explaining the majority of the variation. Covariations between longitude, environmental and spatial variables predominantly shaped β-diversity, and environmental effects explained more variation than any other pure effect type, i.e. environmental sorting explained more variation than dispersal limitation by distance. As in chapter 2, environmental and spatial effects almost equally shaped composition, but covariations between effect types explained more of the variation. Biogeographic variables indicating the degree of site isolation due to biogeographic dispersal barriers explained a minor proportion of variation in composition and no other metric. However, once the contribution of longitudinal and/or latitudinal variation was removed, spatial effects predominantly explained taxonomic diversity. Previous research, in addition to this study, has shown that species richness is geographically dependent in Madagascar (e.g., Ganzhorn et al. 1998, 1999; Lees et al. 1999; Vences et al. 2009). Therefore, the importance of spatial effects in explaining patterns of taxonomic diversity is not surprising. Consistent with Beaudrot and Marshall (2010), this study also found β-diversity was explained predominantly by environmental sorting. However, once the effect of longitude was removed, spatial effects operating at broad spatial scales explained the majority of variation in patterns of primate species

turnover. The spatially explicit modelling approach used in this study showed that spatial structures, which characterize environmental variation and the distance between sites, shape patterns of taxonomic diversity patterns in conjunction with environmental variables leading to patterns of species sorting. Chapter 2 tested the relative contribution of dispersal limitation to arboreal and terrestrial mammal species in Madagascar and found that dispersal limitation explained more variation in primate and arboreal communities than terrestrial and nonprimate communities. These differences are thought to be due to dispersal limitation being magnified for species constrained to specific habitat types, i.e. arboreal environments. Consequently, spatial structures in diversity patterns emerge because species cannot colonize all environmentally appropriate sites (e.g., Chase 2003; Condit et al. 2002; Potts et al. 2002; Tuomisto et al. 2003). Consequently, assembly of species membership in Malagasy primate communities was due to a combination of dispersal limitation and environmental sorting.

Functional Diversity

A combination of environmental and spatial effects largely explained functional diversity of Malagasy primate communities, contra to expectations. Except for functional richness, which was only explained by environmental effects, variation in the two dispersion measures (FDis and RaoQ) was explained by environmental effects, spatial effects, and the covariation between location, environmental and spatial variables. Similar to the assembly pattern found for taxonomic diversity, a combination of dispersal limitation and environmental sorting explain patterns of functional diversity in Malagasy primate communities. This result was unexpected because the traits investigated in this study were resource-related and should therefore have reflected environmental gradients and resulted in communities of species best adapted to their environment (*sensu* Cronwell et al. 2006; Grime 2006). However, because of the presence of demarcated ecoregions

with varying environmental features in Madagascar, spatial effects and the role of stochasticity have also influenced the functional trait structure of primate communities.

Environmental sorting leads to correlations between functional diversity and environmental variation, where traits are adapted to their environment, however spatial structures exist in trait distributions because of either dispersal limitation and/or environmental autocorrelation. As previously mentioned, feeding guild, locomotion and body size have been found to explain the majority of variation in the trait structure of nonvolant mammal communities, which corresponds with ecoregional variation (Muldoon and Goodman 2010). Consequently, functional diversity is found to vary within environments that are spatially structured, i.e. ecoregions. Functional dispersion had significant spatial structures present at predominantly medium spatial scales, explaining 18.7-20.9% of the variation when not detrended (Table 3.8) and 17.6-20% of the variation when detrended (Table 3.10). Medium spatial scales described spatial structures that existed within an ecoregion (Figure 3.9). Within each functional diversity model, the environmental and spatial covariation was lower than the amount of variation attributed to each effect type. Furthermore, once the effect of location (longitude) was removed functional dispersion measures were significantly explained by both environmental variables (10-13.2%) and spatial variables. Consequently, it is unlikely that environmental autocorrelation is driving functional dispersion patterns; it is more likely that dispersal limitation combined with environmental sorting within ecoregions has contributed to extant patterns of functional dispersion in Malagasy primate communities.

Phylogenetic Diversity

The suite of effect types used to indicate assembly processes tested here weakly explained patterns of phylogenetic diversity in Malagasy primate communities.

Environmental and spatial variables significantly individually explained variation in PDm and NRI, and large components of variation in PDm, MPD, and NRI were due to covariations between environmental variables and spatial attributes. Unexpectedly, biogeographic effective distance ratios did not explain any variation in phylogenetic diversity measures. The phylogenetic age or phylogenetic overdispersion of Malagasy primate communities was not dependent on latitudinal or longitudinal effects, i.e. location was not a significant explanatory variable. The weak model fit for phylogenetic measures of diversity is logical because patterns of phylogenetic diversity (measured as NTI and NRI) did not deviate from random expectations. Consequently, identifying the processes, or variables, that influence extant patterns of Madagascar's primate phylogenetic diversity is complicated by the lack of phylogenetic clustering or significant phylogenetic structures present. Furthermore, a lack of phylogenetic signal in trait data may be typical of island faunas (Losos et al. 2003; Kamilar and Muldoon 2010; Knouft et al. 2006; Webb et al. 2002) due to the contribution of adaptive radiations (Losos 2008; Schuleter 2000; Webb et al. 2002). The combined contribution of the phylogenetic structure of Malagasy primate communities, the contribution of past extinctions, and past adaptive radiations have resulted in varied patterns of community assembly that are difficult to generalize island-wide but which may show discrete patterns at the ecoregion level where PDm and NRI are distinct (cf. Kamilar and Muldoon 2010).

Functional Diversity ≠ Phylogenetic Diversity

A major finding of this study is that phylogenetic and functional diversity are not good proxy measures for each other. For at least Madagascar's primate communities, the study of phylogenetic diversity is not enough to test the role of competition or environmental sorting in the community assembly of primate communities. Instead,

phylogenetic and functional diversity test different aspects of primate diversity in Madagascar, which in this study were non-convergent. The utility of phylogenetic metrics of diversity exist when phylogenetic relatedness is positively correlated with functional similarity, because phylogenetic diversity can be used as a measure of community composition which encompasses both phylogenetic and functional aspects of diversity (e.g., Martin 2002; Hardy and Senterre 2007; Graham and Fine 2008; Swenson 2011; Webb et al. 2002).

Although this chapter is not the first study of the phylogenetic diversity of Madagascar's primate communities, it is the first to test the correlation between phylogenetic diversity and functional diversity (but see Kamilar and Cooper 2013 for species-level analysis), and its concurrent utility for the study of community assembly. Previous work in Madagascar has shown that primate communities are phylogenetically overdispersed with low occurrence in closely related species in each community, suggesting that phylogenetic diversity may not be strongly indicative of functional traits (Kamilar and Guidi 2010; Kamilar et al. 2009; Ossi and Kamilar 2006). Closely related Malagasy primate species occupy different climatic niches, and distantly related species share climatic niches (Kamilar and Muldoon 2010). Furthermore, Malagasy primate body mass is highly phylogenetically conserved, and not related to resource or climatic effects (Kamilar et al. 2012). In this study functional and phylogenetic diversity were not strongly correlated ($r < |0.515|$, Table 3.3), suggesting that as previously suggested they are not good proxy measures for each other. These results are congruent with previous work showing overall no correlation between climatic niche and phylogenetic diversity in Madagascar's primates, except for the Indriids (Kamilar and Muldoon 2010), and limited evidence for phylogenetically conserved ecological and climatic niche axes in primates (Kamilar and Cooper 2008).

The poor relationship between phylogenetic and functional diversity measures has implications for the study of assembly and the evolution of communities in the fossil record. Circular assignments of diversity based on the commonly held assumption that closely related species are functionally related (Darwin 1859; Fleagle and Reed 1999; Webb et al. 2002) may lead to spurious results. Although ubiquitous assembly patterns across diversity measures did not exist for extant Malagasy primate communities, functional dispersion (FDis and RaoQ) did have patterns of community assembly that were similar to those observed for β-diversity and composition. Furthermore, functional diversity measures provided better model fits than phylogenetic diversity measures, and better model fits than alpha diversity and composition. Between 47.3% (detrended) and 70.5% (nondetrended) of the variation in functional dispersion was explained. The study of functional diversity in fossil taxa may therefore provide less biased, independent of taxonomic assignments, and yet highly descriptive assembly models (e.g., Dineen et al. 2014; Razafindratsima et al. 2013). The measures of functional diversity used in this study are applicable to fossil fauna where trait data are easier to collect and assign confidently to specimens than phylogenetic or taxonomic data (e.g., Dineen et al. 2014), and where occurrence data are easier to obtain than abundance data. Furthermore, these metrics can include missing data (minimized as much as possible; Pakeman 2014), categorical and quantitative data, and are not computationally expensive.

Diversification and Extinction Effects on Assembly

The current pattern of primate community structure in Madagascar may be strongly influenced by the recent (~2000-2500 years ago) large-scale stepwise cascade of extinctions of numerous mammal species, including primates, with the arrival of humans in Madagascar (Burney et al. 2004; Ganzhorn 1997; Kamilar and Guidi 2010;

Razafindratsima et al. 2013; Richard and Dewar 1991). Extinct subfossil lemurs included many sympatric congeners with similar traits to extant species, including large body size and folivorous diets (e.g., Razafindratsima et al. 2013). All endemic species greater than 10kg went extinct (Burney and MacPhee 1988; Crowley 2010), comprising 29 species of which 17 were primates (IUCN 2014). The loss of these species is predicted to be a potential influence on the extant pattern of overdispersion and niche differentiation within Madagascar's primate communities that are not found in other countries, where recent extinctions of similar magnitude have not occurred (Kamilar and Guidi 2010; Razafindratsima et al. 2013). Differences in traits (body mass, activity period, and diet) between present and Holocene primate communities may reflect the role of recent extinctions (Razafindratsima et al. 2013) and therefore have cascading effects on detected patterns of community assembly.

Trait reconstructions of past primate communities in Madagascar (e.g., Razafindratsima et al. 2013) suggest that the distribution of body masses was decreased and feeding guild diversity increased in extant primate communities with the extinction of 17 subfossil primate species. Selective pressures resulting from the selective extinction of the largest lemur species due to the combined contribution of human hunting, climate change and habitat modification (Burney et al. 2004) has contributed to decreased body size distributions in extant primate communities (Razafindratsima et al. 2013). The more diverse feeding guilds present in extant communities are postulated to be the result of stronger competitive pressures between smaller-bodied primate species leading to dietary niche separation (Razafindratsima et al. 2013). It is feasible that past primate communities were characterized by higher functional diversity values due to the magnitude of body size differences in subfossil lemurs. However, the presence of more diurnal and folivorous/frugivorous species in subfossil than extant communities may have

an averaging effect on functional diversity values resulting in nonsignificant changes in community-level diversity values between extinct and extant communities. However, that is not to say that the predicted assembly patterns would not change. The arrival of humans led to a cascade of environmental changes (Burney et al. 2004) that shaped extant primate communities, in which case environmental sorting would explain more variation in extant communities than extinct. Contrastingly, the decreased habitat availability that characterizes modern Madagascar constrains arboreal primate species to discrete habitat patches and can result in higher levels of dispersal limitation or spatial structuring in their distributions (chapter 2). Consequently, instead of the extinction of 29 species in Madagascar driving extant community assembly patterns the combination of environmental change and intraregional landscape structures has led to a novel competitive landscape resulting in widespread functional, taxonomic, and phylogenetic diversification that ongoing anthropogenic modification compounds. Patterns of extant primate diversity reflect previously recognized patterns of species endemism (Martin 1972; Wilmé et al. 2006; Wilmé and Callmander 2006; but see Raxworthy and Nussbaum 1996) that are associated with elevational changes and latitude (Vences et al. 2009), a history of rapid adaptive radiation (Horvath et al. 2008), the role of riverine barriers and watershed retreats (Vences et al. 2009), novel functional adaptations (e.g., torpor, life history patterns) to specific environmental types (Dewar and Richard 2007; Wright 1999) and anthropogenic disturbance (Schwitzer et al. 2011). Malagasy primate communities appear to have evolved adaptations to particular habitat types that are demarcated by ecoregional boundaries characterized by climatic and floristic differences. The differences between the various habitat types in Madagascar have resulted in unique environments with differentiated resource types allowing for niche differentiation in primate communities, and consequently patterning taxonomic, and functional diversity.

The previously acknowledged poor correlation between phylogenetic and functional diversity measures may be typical of island faunas (Knouft et al. 2006; Kamilar and Muldoon 2010; Losos et al. 2003; Webb et al. 2002) due to the contribution of adaptive radiations (Losos 2008; Schuleter 2000; Webb et al. 2002). In contrast to primate communities in mainland Africa and Asia, Malagasy and South American communities have more balanced phylogenies indicating explosive radiations post-colonization and monophyletic groups (Fleagle and Reed 1999). The nonvolant mammal fauna of Madagascar is 54% primate species (chapter 2), and competition between primate species may be more severe in Madagascar than other regions (Ganzhorn 1999) resulting in extant patterns of primate communities composed of distantly related species that have converged on similar traits. Additionally, a phylogenetic analysis of Malagasy primate communities, Kamilar and Guidi (2010) found that communities are less likely to contain many closely related species (phylogenetic overdispersion) compared to other regions, which they argued could be due to past competition structuring community membership. However, their supposition requires closely related species to also be functionally related and actively competing. While the values of NTI and NRI in this study did not deviate from random expectations, their negative values indicated phylogenetic overdispersion (Webb et al. 2000, 2002; *sensu* Kamilar and Guidi 2010), consistent with previous studies (Kamilar and Guidi 2010; Razafindratsima et al. 2013). This study also found that functional and phylogenetic diversity were weakly related in Malagasy primate communities. A species-level study of 31 traits in primates also found weak phylogenetic signal in many traits, with only brain size exhibiting a high phylogenetic signal (Kamilar and Cooper 2013). Consequently it is unlikely that competition is driving the phylogenetic diversity of Malagasy primate communities. It is also unlikely that the extinction of subfossil lemur species has resulted in extant

phylogenetic patterns in Malagasy primate communities because subfossil and extant Malagasy primate communities have the same patterns of phylogenetic overdispersion (Razafindratsima et al. 2012). Furthermore, identifying the assembly processes that result in phylogenetic overdispersion is complicated because overdispersion can be produced by multiple assembly processes (Kembel 2009; Pavoine and Bonsall 2011). Instead, rapid diversification and adaptive radiations post-colonization is a more likely cause for extant patterns of phylogenetic structure in Madagascar's primate communities.

The arrival and diversification of species can also influence the diversity of communities through priority effects, where early arriving species have a competitive advantage by establishing a large population (Booth and Larson 1999; Chase 2003). However, priority effects have been generally found to be more prominent in higher productivity environments (Chase 2010). While they have not yet been investigated for primate communities, the impact of recent large-scale primate extinctions in Madagascar (Razafindratsima et al. 2013) and the absence of significant biogeographic effects in this study suggest that priority effects are unlikely the driving process behind observed patterns of extant primate diversity

Study Considerations and Future Research

Ecological communities are complex and potentially described by a variety of metrics encapsulating several components of diversity at a variety of scales (e.g., Calba et al. 2014; Kembel 2009; Pavoine and Bonsall 2011). The primate community data used in this study was at a relatively large spatial grain, where the role of fine-scale local processes may be difficult to reveal or identify. Consequently, only medium and broad spatial scale structures were identified, highlighting the need for more primate census data at finer spatial scales, including studies of fine-scale niche separation and

environmental sorting. Studies at finer spatial scales may also reveal different diversity correlations. For example, in a Neotropical dry forest clustering of functional traits varied with spatial scales and had varied relationships with phylogenetic diversity (Swenson and Enquist 2009). Understanding the role of temporal scale in addition to spatial scale is important for revealing the role of historic processes and for determining the degree of constancy present in assembly processes (e.g., Chase 2003; Hein and Gillooly 2011; Schrama et al. 2012).

Diversity patterns are also variably dependent upon alpha diversity due to sampling effects, i.e. higher species richness equals higher trait and phylogenetic richness (Palmer 1991; Rosenzweig 1995). In addition, species richness is thought to be dependent upon area effects resulting in species-area relationships (SARs; Rosenzweig 1995). In this study, I tested diversity dependence between all measures of diversity, and tested the contribution of species-area models on detected patterns of diversity. Furthermore, since sampling was constrained to protected areas the time since protection began in each site was also tested as a corollary of diversity patterns. Primate community diversity in Madagascar was not strongly correlated with species richness, except for one measure of phylogenetic diversity (PDm; Table 3.3). Furthermore, community species richness did not depend upon the protected area size, or age (Table 3.4). These results do not suggest that additional sampling factors or protected area variables do not influence extant primate community diversity. They do, however, highlight the superseding importance of the spatial structuring of environmental variation within Madagascar on patterns of primate diversity, which was supported by the assembly processes detected in this study.

Using a modelling framework to identify the contribution of assembly process to patterns of diversity requires appropriate variable selection. My measure of site isolation

(biogeographic effects) did not explain patterns of taxonomic, functional or phylogenetic diversity in Malagasy primate communities. The reasons for this result (as suggested in chapter 2) include (1) potential error in assigning cost values to barriers used to generate dispersal surfaces, (2) the effect of rivers and water bodies as biogeographic barriers may be too species-specific to see at a community level and biogeographic effective distance had an averaging effect by looking at entire communities, and (3) my analysis may have concealed the effect of the few and significant biogeographic barriers that exist.

In addition, more data are needed on trait variation in primates. The traits utilized in this study were general descriptors of niche axes and for the most part categorical. Previous research on functional diversity suggests that continuous trait data may be preferable (e.g., Petchey and Gaston 2006). Furthermore, single traits can be indicative or strongly correlated with many other traits, for example body mass correlates with many other biological traits (Clutton-Brock and Harvey 1977, 1983), and how these correlations influence depicted niche axes needs to be better understood (*sensu* Spasojevic and Suding 2012). The theory behind inferring community assembly from functional diversity is still developing (Spasojevic and Suding 2012), and requires detailed knowledge about how and which traits relate to each assembly process (Diaz et al. 1999; Violle et al. 2007). Research with plant communities has the advantage of utilizing experimental approaches to test trait variability among species and communities to identify which assembly processes are operating. However, the conservation status of primate communities and the difficulty in designing such experimental approaches with large-bodied long-lived mammals does not allow for such studies. Consequently, the study of functional diversity in vertebrate taxa will have to be repeatedly investigated and discussed as more theory, data, and methodological approaches become available.

The phylogenetic assignments of Madagascar's lemurs have been highly variable over the last decade and influenced by "lumper" versus "splitter" approaches (Tattersall 2007; Mittermeier et al. 2010). In the latter case, a proliferation of subspecies designations have resulted based on either geographic isolation of sub-populations or genetic markers (e.g., Andriaholinirina et al. 2006; Craul et al. 2007; Olivieri et al. 2007; Pastorini et al. 2001). While a potential critique of the use of phylogenetic metrics in this study may be the use of a single phylogeny, previous research has found that the choice of phylogeny for primates does not significantly change measures of NTI and NRI (Kamilar and Guidi 2010; Kamilar et al. 2014). Consequently, unless large-scale changes to Lemuriformes phylogeny occur, the phylogenetic results are unlikely to change.

Conclusions

Patterns of taxonomic, functional and phylogenetic diversity in Malagasy primate communities were geographically variable and explained by a combination of environmental sorting and dispersal limitation by distance. Latitude- (east versus west) and ecoregion- specific patterns in diversity were found for taxonomic, functional and phylogenetic diversity. Eastern Madagascar and the humid ecoregions had higher species richness and lower functional diversity values. Eastern communities were also characterized by older species and distantly related co-occurring species. Biogeographic dispersal barriers leading to site isolation explained only a minor proportion of variation in composition. As predicted, both environmental sorting and dispersal limitation shaped taxonomic diversity. Unexpectedly, functional diversity was also predominantly shaped by environmental sorting and dispersal limitation. Phylogenetic diversity was variably shaped by environmental and spatial effects. For all three diversity types covariations between location, environmental variables and spatial variables explained large

proportions of variation in diversity measures. Ecoregional differences strongly contribute to the observed patterns of environmental sorting and dispersal limitation with clear bioclimatic differences present in Madagascar. Madagascar's primate communities are the result of widespread diversification into novel habitats and the combined action of deterministic and stochastic assembly processes shaping the taxonomic and functional diversity of communities. Continued research into temporal changes in assembly over evolutionary time in Madagascar and the role of anthropogenic disturbance and climate change on primate diversity in Madagascar require further investigation. Within and across diversity measures and within and across biogeographic regions differences in diversity exist with mechanistic implications for understanding patterns of assembly, and consequently the evolution and future of primate communities.

Table 3.1. Diversity measures and interpretations of values used in this study.

Measure	Description	Interpretation	References
Taxonomic Measures			
Species Richness (Alpha (α))	Number of species present at each location; a measure of α.	n/a	Whittaker 1972
Composition	Identity and occurrence (presence-absence) of each species at each location.	n/a	
Jaccard Index (Beta (β)) [1]	A presence-based index expressing differences in diversity between locations with a value between 0 and 1; a measure of β.	Community pairs with values close to zero are dissimilar in composition, communities with values close to one share similar species composition.	Jaccard 1901; Whittaker 1972
Functional Measures			
Functional Richness (FRic)	Describes the amount of niche space filled by the species in a community; measured as a convex hull volume of functional space.	Smaller values (close to 0) indicate smaller hull volumes and smaller absolute functional space occupied by the community, and vice versa.	Cornwell et al. 2006; Mason et al. 2005; Villéger et al. 2008
Functional Divergence (FDiv)	The total community variation in traits determined by the distribution of species abundances in niche space; independent from and orthogonal to FRic.	High values (close to 1) indicate a high degree of niche differentiation (low competition), and vice versa.	Mason et al. 2005; Mouchet et al. 2010; Villéger et al. 2008
Functional Dispersion (FDis)	Represents the average distance of species in multidimensional space from a centroid defined by a distance matrix, i.e. the mean distance of species from the community centroid adjusting for occurrence.	High values indicate large distances between species and the community centroid, i.e. large dispersion around the community median value, and vice versa.	Laliberté and Legendre 2010
Rao's Quadratic diversity (RaoQ)	Sum of pairwise functional distances between species; describes components of both FRic and FDiv.	High values indicate large pairwise functional distances, and vice versa.	Botta-Dukat 2005; Rao 1982

Table 3.1 (continued)

Measure	Description	Interpretation	References
Phylogenetic measures			
Phylogenetic diversity measure (PDm)	Characterizes the sum of the total phylogenetic branch length for each community; summary measure of the evolutionary history encompassed by each community.	Higher total branch length indicates a longer evolutionary history, whereas a lower total branch length indicates a shallow evolutionary history.	Faith 1992; Kembel et al. 2010
Mean Pairwise Distance (MPD)	Mean of all pair-wise distances among species in a community; an overall tree-wide measure of phylogenetic clustering and overdispersion.	High values indicate high phylogenetic diversification, and vice versa.	Webb 2000
Mean Nearest Taxon Distance (MNTD)	Average distance separating each species in the community from its closest heterospecific relative, measure of phylogenetic overdispersion or clustering at the tips of a phylogeny	High values indicate overdispersion, whereas low values indicate clustering at the tips of the phylogeny.	Webb 2000
Net Relatedness Index (NRI)	Mean phylogenetic distances among all taxa in a community relative to a randomized sample of null communities based upon all the species found in a dataset; based upon measure of MPD.	Positive NRI values and high p-value quantiles (> 0.95) indicate phylogenetic clustering. Conversely, negative NRI values and low quantiles (< 0.05) indicate phylogenetic overdispersion, relative to the null model. Values near zero indicate a phylogenetically random assemblage of species.	Webb et al. 2000, 2002
Nearest Taxon Index (NTI)	Phylogenetic distance among closest related taxa, relative to a randomized sample of null communities constructed from all the species in the dataset; based upon measure of MNTD.	Negative values indicate that closely related taxa do not co-occur, and positive values indicate that they co-occur more than expected by chance. Values near zero indicate a phylogenetically random assemblage of species.	Webb et al. 2000, 2002

[1] This measure is transformed for analysis from a matrix to 2-D space using principal coordinates analysis, where only the positive axes are retained for analysis.

Table 3.2. Hypotheses and predicted diversity patterns from the literature for ecological communities under deterministic, stochastic and biogeographic assembly scenarios. Hypotheses for patterns in diversity expected under each process type are provided for each diversity type (taxonomic, functional, and phylogenetic) and specific predictions are provided for each diversity measure.

	Deterministic Process	**Stochastic Process**	**Biogeographic Process**
Specific Process	• Environmental sorting	• Dispersal limitation by distance	• Biogeographic dispersal barriers
Taxonomic Diversity	Patterns of diversity are homogeneous in environmentally similar sites and heterogeneous with environmental gradients or environmental heterogeneity. Patterns in diversity sort with environmental variables (Chase 2003, 2007; Chase and Myers 2011).	Patterns of diversity are geographically homogeneous where sites are close together and between-site dispersal is high (Hubbel 2001; cf. Loreau and Mouquet 1999; Mouquet and Loreau 2003).	Patterns of diversity are geographically homogeneous where sites are bounded by the same biogeographic barriers, and heterogeneous due to past patterns of allopatric speciation or different species present between areas bounded by biogeographic barriers (Simpson 1953; Tokeshi 1999; Vences et al. 2009).
Species Richness/Alpha (α)	(1) Equal values in environmentally similar sites.	(1) High values in geographically close sites and between-site dispersal is high.	(1) High values in sites bound by the same biogeographic barriers/site isolation is low.
	(2) Dissimilar values in environmentally different sites.	(2) Low values geographically far sites or between-site dispersal is low.	(2) Low values in sites separated by biogeographic barriers/site isolation is high.
Beta (β)	(1) Low values in environmentally similar sites.	(1) Low values geographically close sites and between-site dispersal is high.	1) Low values in sites bound by the same biogeographic barriers/site isolation is low.
	(2) High values in environmentally different sites.	(2) High values in geographically far sites or between-site dispersal is low.	(2) High values in sites separated by biogeographic barriers/site isolation is high.
Composition	(1) Species lists are similar in environmentally similar sites.	(1) Species lists are similar in geographically close sites.	(1) Species lists are similar in sites bound by the same biogeographic barriers/site isolation is low.
	(2) Species lists are different in environmentally different sites.	(2) Species lists are different in geographically far sites.	(2) Species lists are different in sites separated by biogeographic barriers/site isolation is high.

Table 3.2 (continued)

Specific Process	**Deterministic Process** • Environmental sorting	**Stochastic Process** • Dispersal limitation by distance	**Biogeographic Process** • Biogeographic dispersal barriers
Functional Diversity	Patterns of diversity strongly correlate with environmental conditions (Cornwell et al. 2006; de Bello et al. 2005; Diaz et al. 1998; Diaz and Cabido 2001; Grime 2006; Lessard et al. 2012). Environmental sorting limits the range of viable traits, resulting in decreased functional divergence/dispersion within similar environments and increased divergence/dispersion between different environments (Cornwell et al. 2006; de Bello et al. 2005; Diaz and Cabido 2001; Grime 2006; Holdoway and Sparrow 2006; Lessard et al. 2012; Pierce et al. 2007; Siefert 2012; Vivian-Smith 1997; Weiher et al. 1998).	Due to the homogenizing effect of dispersal patterns are spatially structured (Mouquet and Loreau 2003; Münkemüller et al. 2012) and communities connected by dispersal are functionally similar to each other (Hubbell 2001; Holyoak et al. 2005; Mouquet and Loreau 2003; Münkemüller et al. 2012; Siefert 2012). Alternatively, if species are functionally equivalent and disperse randomly, functional trait values are randomly distributed in space, and functional diversity will not depend on the spatial distance separating them (Hubbel 2001).	Functional diversity is geographically homogeneous where sites are bounded by the same biogeographic barriers, and heterogeneous due to past patterns of allopatric speciation or different species present between areas bounded by biogeographic barriers (cf. Tokeshi 1999).
Functional Richness (FRic)	(1) Low values (small hull volume) with environmental homogeneity. (2) High values (large hull volume) with environmental heterogeneity.	(1) Values are spatially structured, and similar functional richness values exist in geographically close sites. (2) Species are functionally equivalent and values are randomly structured.	(1) Equal values in sites bound by the same biogeographic barriers/site isolation is low. (2) Different values, or high values (large hull volume) in sites separated by biogeographic barriers/site isolation is high.
Functional Divergence (FDiv)	(1) Low values (close to 0) with environmental homogeneity. (2) High values (close to 1) with environmental heterogeneity.	(1) Low values (close to 0) in geographically close sites. (2) High values (close to 1) in geographically far sites or with random dispersal/functional equivalence.	(1) Low values (close to 0) in sites bound by the same biogeographic barriers/site isolation is low. (2) High values (close to 1) in sites separated by biogeographic barriers/site isolation is high.

Table 3.2 (continued)

Specific Process	**Deterministic Process** • Environmental sorting	**Stochastic Process** • Dispersal limitation by distance	**Biogeographic Process** • Biogeographic dispersal barriers
Functional Dispersion (FDis)	(1) Low values (low dispersion) with environmental homogeneity. (2) High values (high dispersion) with environmental heterogeneity.	(1) Low values (low dispersion) within spatially clustered or nearby sites that allow for dispersal between sites. (2) High values (high dispersion) or no patterning in values in geographically far apart sites or with random dispersal/functional equivalence.	(1) Low values (low dispersion) in sites bound by the same biogeographic barriers/site isolation is low. (2) High values (high dispersion) in sites separated by biogeographic barriers/site isolation is high.
Rao's Quadratic Entropy (RaoQ)	(1) Low values (small pairwise functional differences) with environmental homogeneity. (2) High values (large pairwise functional differences) with environmental heterogeneity.	(1) Low values (small pairwise functional differences) in geographically close sites. (2) High values (large pairwise functional differences) or no patterning in values in geographically far sites or with random dispersal/ functional equivalence.	(1) Low values (small pairwise functional differences) in sites bound by the same biogeographic barriers/site isolation is low. (2) High values (large pairwise functional differences) in sites separated by biogeographic barriers/site isolation is high.
Phylogenetic Diversity	Habitat specialization and environmental filtering lead to phylogenetic clustering when traits that provide an environmental advantage are phylogenetically conserved (Webb et al. 2002; Cavender-Bares et al. 2004). Alternatively, if traits promoting habitat specialization evolve convergently, environmental filtering causes phylogenetic overdispersion (Cavender-Bares et al. 2009; Kembel 2009; Webb et al. 2002).	Dispersal limitation causes spatial clustering of phylogenetically similar individuals (Eiserhardt et al. 2013; Graham et al. 2009; Levine and Murrell 2003).	Patterns of phylogenetic diversity are geographically homogeneous where sites are bounded by the same biogeographic barriers, and heterogeneous due to past patterns of allopatric speciation or different species present between areas bounded by biogeographic barriers (Simpson 1953; Tokeshi 1999; Vences et al. 2009).

Table 3.2 (continued)

	Deterministic Process	**Stochastic Process**	**Biogeographic Process**
Specific Process	• Environmental sorting	• Dispersal limitation by distance	• Biogeographic dispersal barriers
Phylogenetic Diversity measure (PDm)	(1) High values (deep) where environmental heterogeneity is low. (2) Low values (shallow) where environmental heterogeneity is high due to adaptive radiations.	(1) High values (deep) where dispersal between sites is low or in geographically far sites. (2) Low values (shallow) where dispersal between sites is high due or in geographically close sites.	(1) High values (deep) in sites bound by the same biogeographic barriers/site isolation is low. (2) Low values (shallow) in sites separated by biogeographic barriers/site isolation is high.
Mean Pairwise Distance (MPD)	(1) Low values (phylogenetic clustering) when conserved characters determine environmental sorting. (2) High values (indicating phylogenetic overdispersion) when convergent characters determine environmental sorting.	(1) Low values (low diversification) in geographically close sites. (2) High values (high diversification) in geographically far sites.	(1) Low values (low diversification) in sites bound by the same biogeographic barriers/site isolation is low. (2) High values (low diversification) in sites separated by biogeographic barriers/site isolation is high.
Mean Nearest Taxon Distance (MNTD)	(1) Low values (phylogenetic clustering) when conserved characters determine environmental sorting. (2) High values (indicating phylogenetic overdispersion) when convergent characters determine environmental sorting.	(1) Low values (phylogenetic clustering) in geographically close sites. (2) High values (indicating phylogenetic overdispersion) in geographically far sites.	(1) Low values (phylogenetic clustering) in sites bound by the same biogeographic barriers/site isolation is low. (2) High values (indicating phylogenetic overdispersion) in sites separated by biogeographic barriers/site isolation is high.
Net Relatedness Index (NRI)	(1) NRI>0 (phylogenetic clustering) when conserved characters in closely related species determine environmental sorting. (2) NRI<0 (phylogenetic overdispersion) when convergent characters due to rapid divergence among close relatives determine environmental sorting.	(1) NRI>0 (phylogenetic clustering) in geographically close sites. (2) NRI<0 (phylogenetic overdispersion) in geographically far sites.	(1) NRI>0 (phylogenetic clustering) in sites bound by the same biogeographic barriers/site isolation is low. (2) NRI<0 (phylogenetic overdispersion) in sites separated by biogeographic barriers/site isolation is high.

Table 3.2 (continued)

	Deterministic Process	**Stochastic Process**	**Biogeographic Process**
Specific Process	• Environmental sorting	• Dispersal limitation by distance	• Biogeographic dispersal barriers
Nearest Taxon Index (NTI)	(1) NTI>0 (phylogenetic clustering) when conserved characters in closely related species determine environmental sorting. (2) NTI<0 (phylogenetic overdispersion) when convergent characters due to rapid divergence among close relatives determine environmental sorting.	(1) NTI>0 (phylogenetic clustering) in geographically close sites. (2) NTI<0 (phylogenetic overdispersion) in geographically far sites.	(1) NTI>0 (phylogenetic clustering) in sites bound by the same biogeographic barriers/site isolation is low. (2) NTI<0 (phylogenetic overdispersion) in sites separated by biogeographic barriers/site isolation is high.

Table 3.3. Linear regressions of diversity measures on primate species richness (alpha diversity) in Madagascar. Log linear regressions are not reported as they showed similar trends. Adjusted R^2 values are shown with a "+" or "-" in parentheses to indicate the direction of the linear trend, if significant.

Diversity Measure	Adj. R^2	p-value
Beta (1st PCoA Axis)	0.262 (+)	0.001
FRic	-0.026	0.693
FDis	0.297 (-)	<0.000
FDiv	0.035	0.148
RaoQ	0.293 (-)	<0.000
PDm	0.889 (+)	<0.000
MPD	<0	0.678
MNTD	0.419 (-)	<0.000
NRI	0.088 (-)	0.049
NTI	0.564 (-)	<0.000

Abbreviations: β, beta diversity; FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index.

Table 3.4. Alpha diversity relationships with the size of the protected area (Area) and the duration of protection (Age) for 34 primate communities in Madagascar. Area and age data are available in Table A.3.

	Area		Age
Model	**Summary statistics**	**AIC**	**Summary statistics**
Linear model	t=0.205 p=0.839 adj.R^2=-0.030	167.459	t=-0.545 p=0.590 adj.R^2=-0.022
Arrhenius (Power) model [1]	t=0.592 p=0.558	167.111	nt
Log-Arrhenius model	t=0.933 p=0.358 adj.R^2=-0.004	30.191	nt
Gleason (log-log linear) model	t=0.616 p=0.542 adj.R^2=-0.019	167.103	nt

nt, not tested. Degrees of freedom for all models was 32.
[1] summary statistics reported for the z value (the exponent) in the model; no adj.R^2 provided

Table 3.5. Forward selection of variables and RDA results for non-linearly detrended primate diversity in Madagascar. Beta diversity is measured as the first PCoA axis of the Jaccard index.

		ANOVA of global RDA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj. R^2**	***F*-value**	***p*-value**
Alpha	Location	4.302	0.025	Longitude	0.192	8.861	0.005
	Environment	4.365	0.008	AnnPrecip	0.225	10.586	0.003
	Protected Area	1.1962	0.21	n/a			
	Biogeography	1.787	0.165	n/a			
	Spatial (PCNMs)	4.692	0.003	PCNM4	0.134	6.111	0.028
				PCNM2	0.245	5.728	0.018
				PCNM8	0.321	4.457	0.044
				PCNM10	0.391	4.459	0.045
Comp.	Location	6.437	<0.000	Longitude	0.194	8.946	0.001
				Latitude	0.248	3.287	0.001
	Environment	4.146	0.001	AnnPrecip	0.171	7.791	<0.000
				TempSeas	0.251	4.460	<0.000
				Elevation	0.296	2.948	<0.000
				AnnTemp	0.323	2.209	<0.000
	Protected Area	0.144	0.871	n/a			
	Biogeography	1.726	0.005	Edge DR	0.048	2.659	0.033
	Spatial (PCNMs)	3.528	<0.000	PCNM2	0.136	6.198	0.001
				PCNM1	0.219	4.395	0.001
				PCNM5	0.275	3.415	0.001
				PCNM6	0.318	2.889	0.001
				PCNM4	0.364	3.088	0.002
				PCNM3	0.403	2.832	0.001
				PCNM7	0.420	1.801	0.035
Beta	Location	38.533	0.001	Longitude	0.697	76.750	0.001
	Environment	35.918	<0.000	AnnPrecip	0.609	52.399	<0.000
				TempSeas	0.850	52.594	<0.000
	Protected Area	1.958	0.150	n/a			
	Biogeography	2.178	0.110	n/a			
	Spatial (PCNMs)	20.149	<0.000	PCNM2	0.474	30.732	0.001
				PCNM1	0.676	21.038	0.001
				PCNM5	0.771	13.817	0.002
				PCNM4	0.817	8.473	0.007
				PCNM3	0.837	4.519	0.042
FDiv	Location	0.176	0.858	n/a			
	Environment	0.391	0.857	n/a			
	Protected Area	1.371	0.249	n/a			
	Biogeography	0.605	0.597	n/a			
	Spatial (PCNMs)	1.621	0.170	n/a			
FRic	Location	5.621	0.004	Longitude	0.241	11.475	0.001
	Environment	3.550	0.012	PrecipSeas	0.312	15.944	<0.000
	Protected Area	1.111	0.352	n/a			
	Biogeography	2.493	0.085	n/a			
	Spatial (PCNMs)	1.656	0.160	n/a			

Table 3.5 (continued)

		ANOVA of global RDA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj. R^2**	***F*-value**	***p*-value**
FDis	Location	9.002	<0.000	Longitude	0.313	16.021	0.001
	Environment	8.115	<0.000	PrecipSeas	0.287	14.287	<0.000
				Elevation	0.420	8.326	0.006
				TempSeas	0.484	4.842	0.036
	Protected Area	0.169	0.840	n/a			
	Biogeography	1.132	0.354	n/a			
	Spatial (PCNMs)	5.322	<0.000	PCNM1	0.198	9.141	0.008
				PCNM4	0.316	6.521	0.018
				PCNM2	0.419	6.473	0.023
				PCNM8	0.511	6.660	0.014
				PCNM9	0.578	5.628	0.024
RaoQ	Location	11.287	<0.000	Longitude	0.362	19.715	0.001
	Environment	9.424	<0.000	AnnPrecip	0.329	17.164	<0.000
				PrecipSeas	0.455	8.404	0.006
				Elevation	0.512	4.624	0.037
	Protected Area	0.085	0.921	n/a			
	Biogeography	1.156	0.343	n/a			
	Spatial (PCNMs)	6.109	0.003	PCNM1	0.233	11.049	0.002
				PCNM2	0.359	7.283	0.011
				PCNM4	0.467	7.291	0.013
				PCNM8	0.554	6.822	0.017
				PCNM9	0.627	6.677	0.016
PDm	Location	2.458	0.116	n/a			
	Environment	3.253	0.019	AnnPrecip	0.175	8.019	0.008
	Biogeography	0.816	0.520	n/a			
	Protected Area	0.629	0.536	n/a			
	Spatial (PCNMs)	2.797	0.015	PCNM2	0.129	5.873	0.015
				PCNM8	0.227	5.089	0.0300
MPD	Location	1.632	0.201	n/a			
	Environment	3.185	0.029	Elevation	0.122	5.603	0.021
				AnnTemp	0.221	5.040	0.033
				AnnPrecip	0.293	4.190	0.049
	Protected Area	0.050	0.964	n/a			
	Biogeography	0.643	0.600	n/a			
	Spatial (PCNMs)	2.513	0.031	PCNM1	0.250	11.983	0.003
				PCNM3	0.364	6.784	0.015
MNTD	Location	1.387	0.250	n/a			
	Environment	1.696	0.163	n/a			
	Protected Area	1.382	0.277	n/a			
	Biogeography	0.877	0.474	n/a			
	Spatial (PCNMs)	1.906	0.094	n/a			
NRI	Location	4.409	0.008	Latitude	0.181	8.299	0.008
	Environment	3.682	0.009	Elevation	0.199	9.186	0.006
				AnnTemp	0.338	7.754	0.008
	Protected Area	0.069	0.938	n/a			
	Biogeography	1.646	0.226	n/a			
	Spatial (PCNMs)	1.776	0.106	n/a			

Table 3.5 (continued)

		ANOVA of global RDA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj. R^2**	***F*-value**	***p*-value**
NTI	Location	1.701	0.241	n/a			
	Environment	2.172	0.075	n/a			
	Protected Area	2.641	0.094	n/a			
	Biogeography	0.837	0.460	n/a			
	Spatial (PCNMs)	2.051	0.072	n/a			

Abbreviations: α, alpha diversity; β, beta diversity; Comp., composition; FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index; PCNM, Principal Coordinates of Neighbour Matrices; n/a; not applicable because not significant; ns, no variable selected; AnnPrecip, mean annual precipitation; PrecipSeas, precipitation seasonality; AnnTemp, mean annual temperature; TempSeas, temperature seasonality; EdgeDR, edge effective distance ratio.

Table 3.6. Forward selection of variables and RDA results for linearly detrended primate diversity in Madagascar. Beta diversity is measured as the first PCoA axis of the Jaccard index.

		ANOVA of global RDA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj.R^2**	***F*-value**	***p*-value**
Alpha	Environment	2.474	0.058	ns			
	Biogeography	0.421	0.749	n/a			
	Spatial (PCNMs)	3.229	0.013	PCNM4	0.166	7.550	0.007
				PCNM10	0.272	5.697	0.029
				PCNM8	0.384	6.629	0.012
Comp.	Environment	1.541	0.006	PrecipSeas	0.032	2.092	0.005
	Biogeography	1.178	0.181	n/a			
	Spatial (PCNMs)	1.819	<0.000	PCNM4	0.052	2.809	0.001
				PCNM2	0.092	2.405	0.002
				PCNM6	0.132	2.451	0.001
				PCNM3	0.175	2.539	0.002
Beta	Environment	7.394	<0.000	TempSeas	0.308	15.682	<0.000
				AnnTemp	0.376	4.473	0.040
	Biogeography	0.602	0.628	n/a			
	Spatial (PCNMs)	3.345	0.007	PCNM2	0.223	10.465	0.002
				PCNM4	0.331	6.183	0.020
				PCNM1	0.420	5.756	0.014
FRic	Environment	1.457	0.240	n/a			
	Biogeography	2.495	0.079	n/a			
	Spatial (PCNMs)	0.552	0.821	n/a			
FDis	Environment	3.969	0.007	PrecipSeas	0.099	4.648	0.040
				AnnTemp	0.255	7.659	0.010
	Biogeography	0.247	0.856	n/a			
	Spatial (PCNMs)	2.545	0.027	PCNM4	0.159	7.221	0.011
				PCNM8	0.300	7.455	0.009
				PCNM9	0.375	4.712	0.037
RaoQ	Environment	3.775	0.013	AnnTemp	0.092	4.335	0.044
				TempSeas	0.261	8.318	0.006
	Biogeography	0.201	0.906	n/a			
	Spatial (PCNMs)	1.689	0.138	n/a			
NRI	Environment	1.556	0.202	n/a			
	Biogeography	0.956	0.417	n/a			
	Spatial (PCNMs)	1.194	0.353	n/a			

Abbreviations: α, alpha diversity; β, beta diversity; Comp., composition; FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index; PCNM, Principal Coordinates of Neighbour Matrices; n/a, not applicable because not significant; ns, no variable selected; PrecipSeas, precipitation seasonality; AnnTemp, mean annual temperature; TempSeas, temperature seasonality.

Table 3.7. Variation partitioning results for all nondetrended primate diversity measures in Madagascar. Beta diversity is measured as the first PCoA axis of the Jaccard index. Amounts of explained variation are expressed as percentages of pure variation and total variation in parentheses. Significant pure components of variation are denoted by asterisks: $p<0.05$*, $p\leq0.01$**, $p\leq0.001$***

Nondetrended Diversity	Location	Environment	Biogeographic	Spatial	Location ∩ Environment	Environment ∩ Spatial	Remaining Covariation	Explained Variation
Alpha	1.3 (19.2)	<0 (22.5)	nt	28.3** (39.1)	10.1	2.9	10.6	49.4
Beta	<0 (69.7)	5.4** (85.0)	nt	2.7* (83.7)	1.2	2.5	78.4	89.9
Comp.	2.4* (24.8)	5.3** (32.3)	0.2 (4.79)	8.6*** (42.0)	<0	10.1	24.0	49.1
FRic	6.2 (24.1)	13.2** (31.2)	nt	nt	nt	nt	nt	37.3
FDiv	nt	nt	nt	nt	nt	nt	nt	0
FDis	<0 (31.3)	7.2 (48.4)	nt	17.4* (57.8)	0.7	8.5	32.0	64.4
RaoQ	<0 (36.2)	8.6* (51.2)	nt	19.6** (62.7)	0.2	6.2	36.9	70.5
PDm	nt	5.1 (17.5)	nt	10.3* (22.7)	nt	12.4	0	27.8
MPD	nt	<0 (29.3)	nt	3.5 (36.4)	nt	32.9	0	32.8
MNTD	nt	nt	nt	nt	nt	nt	nt	0
NRI	<0 (18.1)	13.5* (33.8)	nt	nt	20.3	nt	0	31.7
NTI	nt	nt	nt	nt	nt	nt	nt	0

Abbreviations: α, alpha diversity; β, beta diversity; Comp., composition; FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index; ∩: indicates the component of shared variation between two sets of explanatory variables (i.e. effect types); nt, not tested because no variables were forward selected to include in the model.

Table 3.8. Variation partitioning results for applicable nondetrended primate diversity measures with broad and medium spatial scale structures in Madagascar. Measures of diversity with spatial proportions of variation in Table 3.6 not reported below have only broad spatial structures (PCNM1-5). Amounts of explained variation are expressed as percentages of pure variation and total variation in parentheses. Significant pure components of variation are denoted by asterisks: $p<0.05$*, $p\leq0.01$**, $p\leq0.001$***

Nondetrended Diversity	Location	Environ.	Broad Scale	Medium Scale	Environ. ∩ Broad	Environ. ∩ Medium	Broad ∩ Medium	Remaining Covariation	Explained Variation
Alpha	2.7 (19.2)	<0 (27.9)	11.5* (24.6)	18.3** (12.1)	3.6	<0	<0	24.5	49.4
Comp.	2.3* (24.8)	4.5* (32.3)	6.6*** (35.4)	4.0** (3.3)	9.6	<0	<0	27.2	48.9
FDis	<0 (31.3)	7.2 (48.4)	2.3 (41.9)	18.7** (11.7)	10.0	<0	<0	34.0	64.4
RaoQ	<0 (36.2)	8.6* (51.2)	1.4 (46.7)	20.9*** (11.4)	10.9	<0	<0	40.6	70.5
PDm	nt	5.1 (17.5)	12.4 (12.9)	9.6* (9.2)	12.3	0.2	<0	0	27.8

Abbreviations: Environ., environment; α, alpha diversity; β, beta diversity; Comp., composition; FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index; ∩: indicates the component of shared variation between two sets of explanatory variables (i.e. effect types); nt, not tested because no variables were forward selected to include in the mode

Table 3.9. Variation partitioning results for applicable detrended primate diversity measures in Madagascar. Amounts of explained variation are expressed as percentages of pure variation and total variation in parentheses. Significant pure components of variation are denoted by asterisks: $p<0.05$*, $p\leq0.01$**, $p\leq0.001$***

Detrended Diversity	Environment	Broad Scale	Medium Scale	Environment ∩ Broad	Environment ∩ Medium	Remaining Covariation	Explained Variation
Alpha	nt	18.3** (13.4)	21.9** (20.1)	nt	nt	<0	38.4
Beta	10.6* (37.6)	15.4* (42.3)	nt	26.9	nt	0	52.9
Comp.	0.1 (3.2)	10.8* **(13.2)	4.1*** (3.5)	3.2	0.1	<0	17.6
FRic	nt	nt	nt	nt	nt	nt	0
FDis	13.2* (25.5)	6.5* (15.9)	20.0** (19.9)	11.1	1.5	<0	50.7
RaoQ	10.0* (26.1)	5.7* (14.4)	17.6* (21.2)	10.3	<0	5.3	47.3
NRI	nt	nt	nt	nt	nt	nt	0

Abbreviations: α, alpha diversity; β, beta diversity; Comp., composition; FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index; ∩: indicates the component of shared variation between two sets of explanatory variables (i.e. effect types); nt, not tested because no variables were forward selected to include in the model

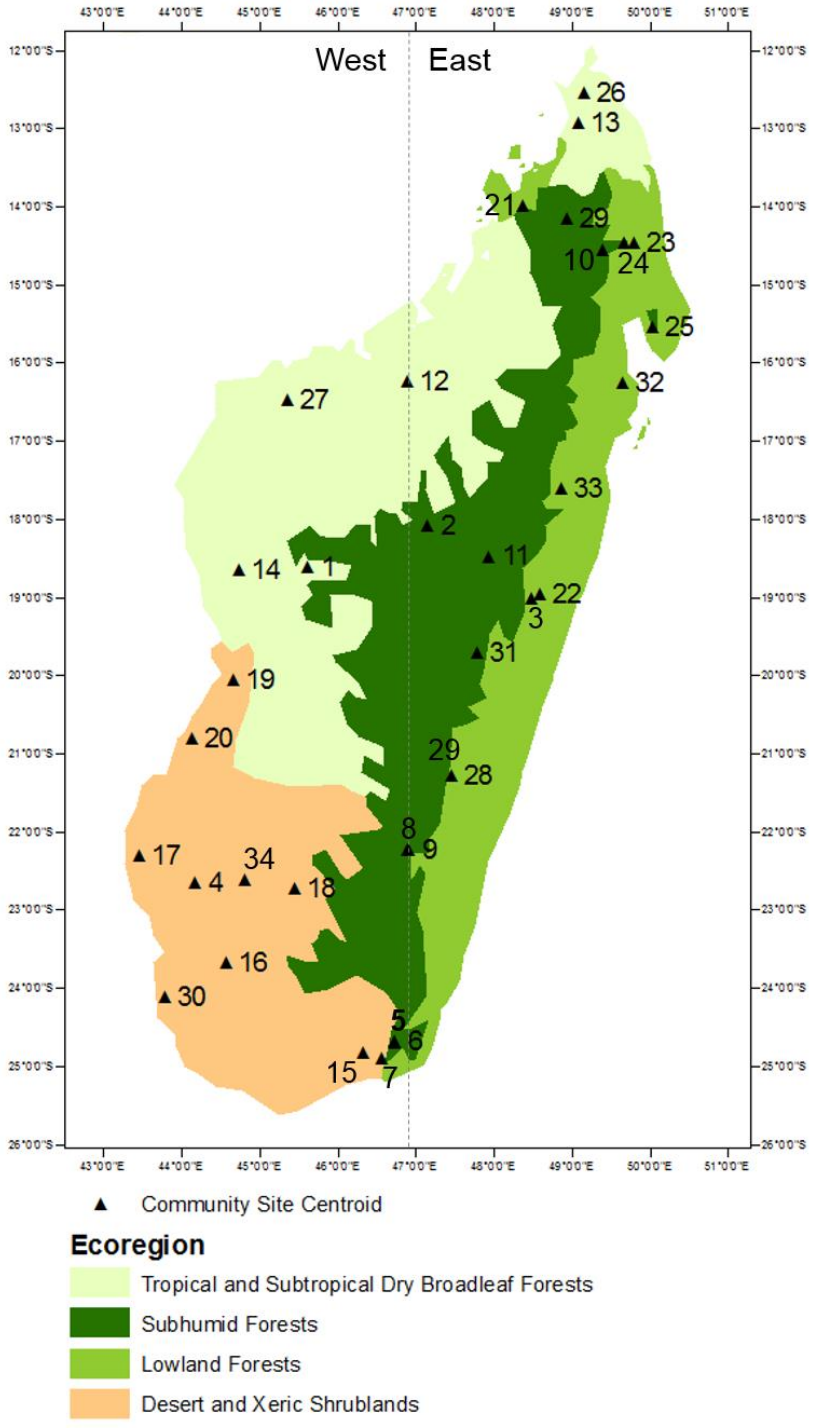


Figure 3.1. Sites included in this study within protected areas in Madagascar with primate communities. Study sites shown as study site centroids within one of four ecoregions (cf. Olson and Dinerstein 2002). Sites were classified as in the west or the east based on a longitude of 46.9º (dashed grey line).

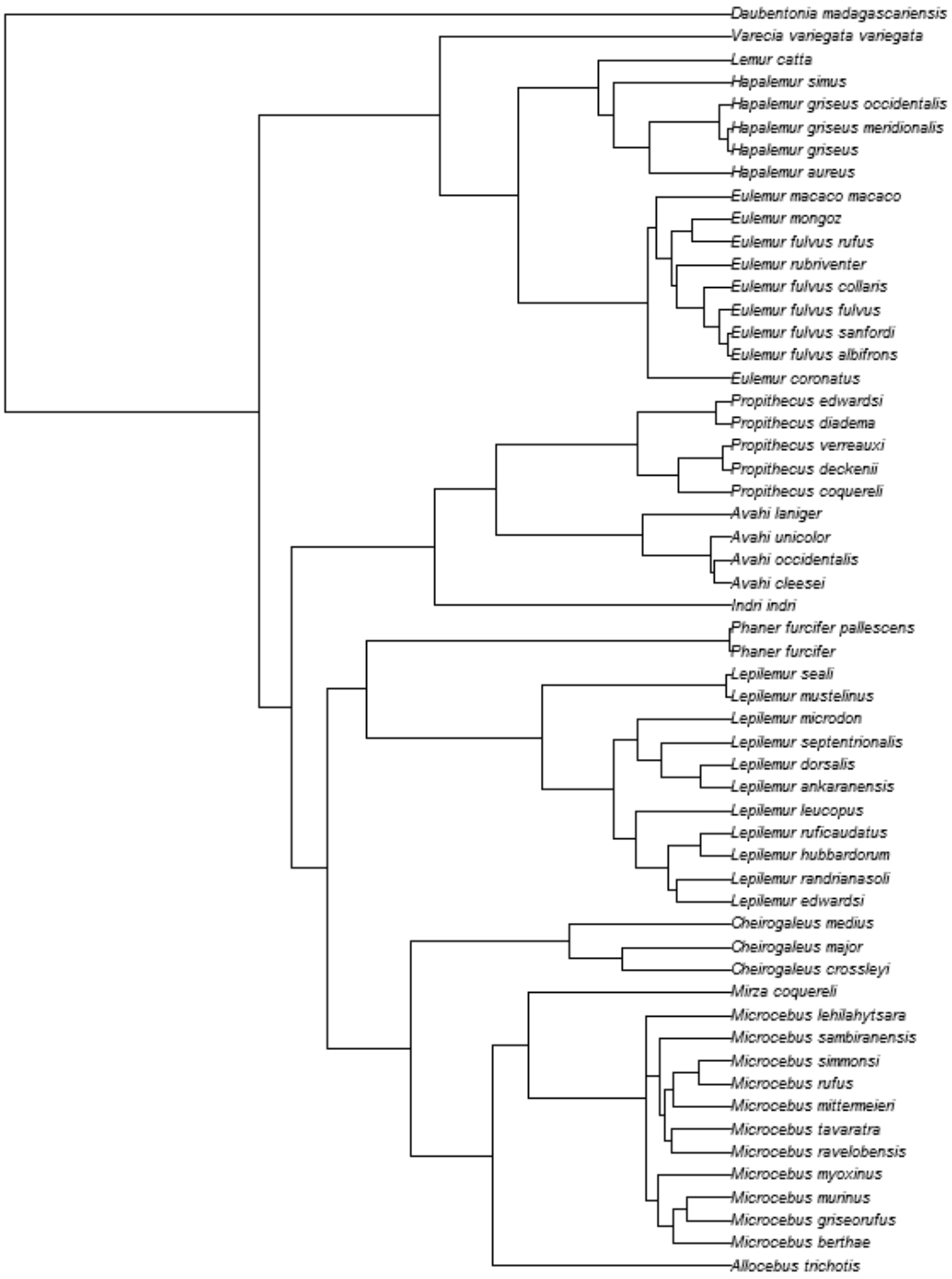


Figure 3.2. Phylogenetic tree for Madagascar's primates from the primate consensus tree in the 10K Trees Project Version 3 (Arnold et al. 2010) and the Genbank taxonomy (Table A.7).

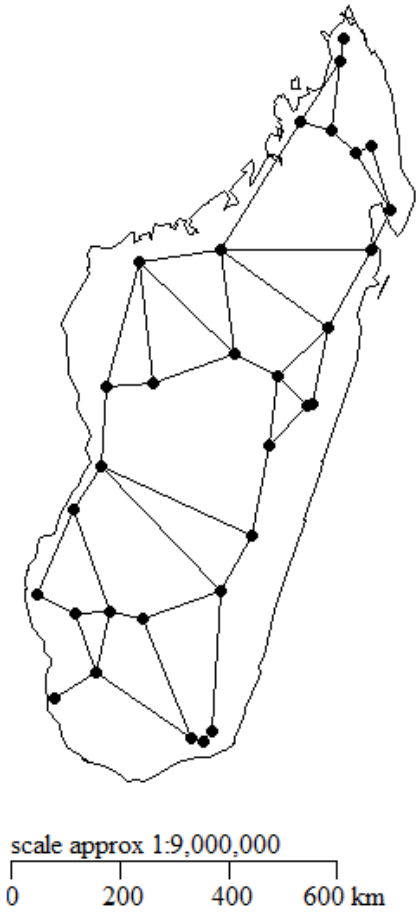


Figure 3.3. The neighbouring graph of study sites for Madagascar's primate communities. Depicts the Euclidean minimum spanning tree of study sites where the total length of the lines connecting sites is minimized, and any site can be reached from any other site by following the lines connecting sites.

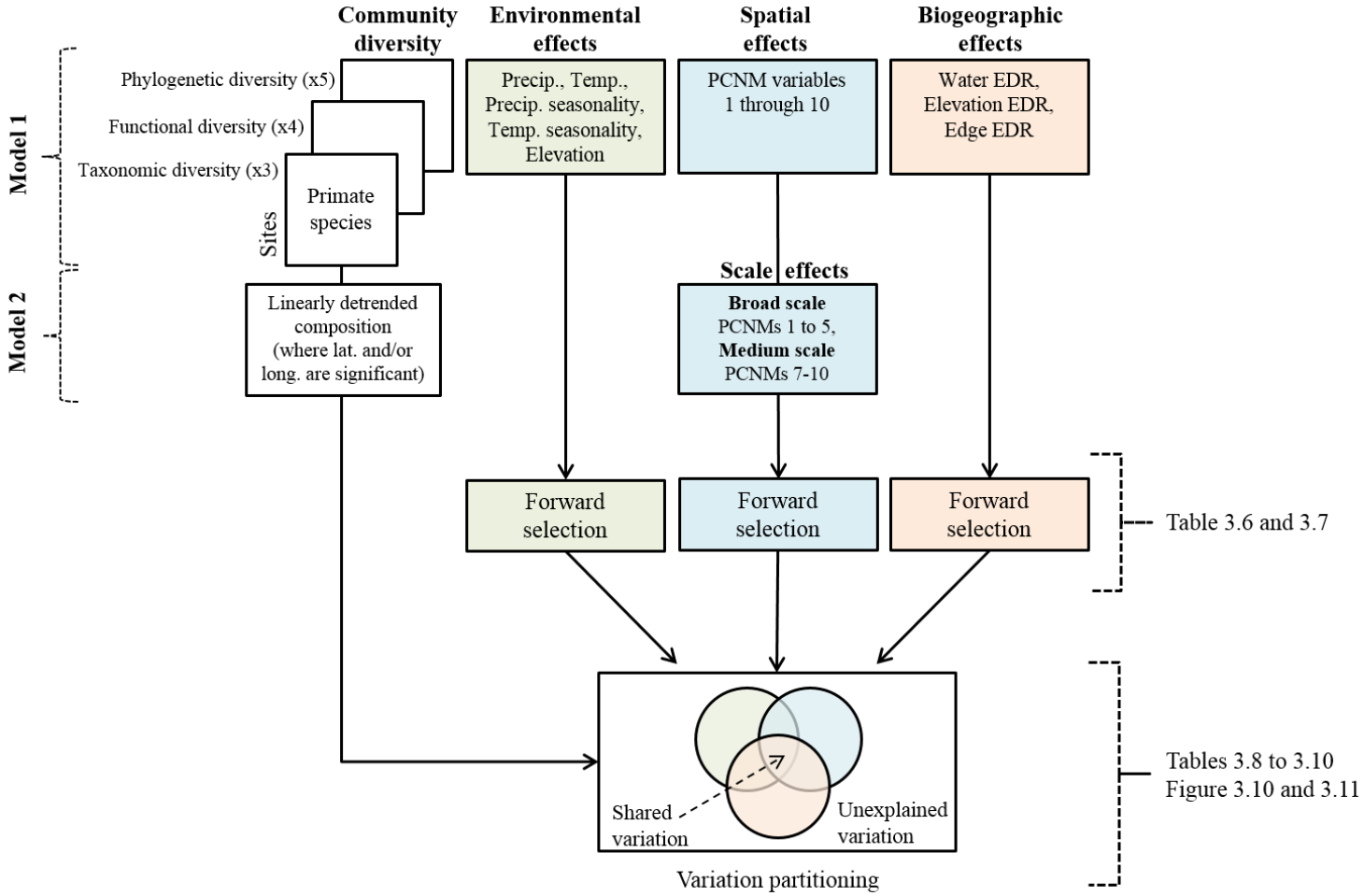


Figure 3.4. Schematic of the different datasets used and the analytical steps performed in this chapter to identify the community assembly processes shaping primate communities in Madagascar. Steps were repeated for each unique diversity measure describing Malagasy primate communities. Results of analyses are provided in indicated tables and figures. This schematic is based on Figure 1.6, the analytical framework for the dissertation.

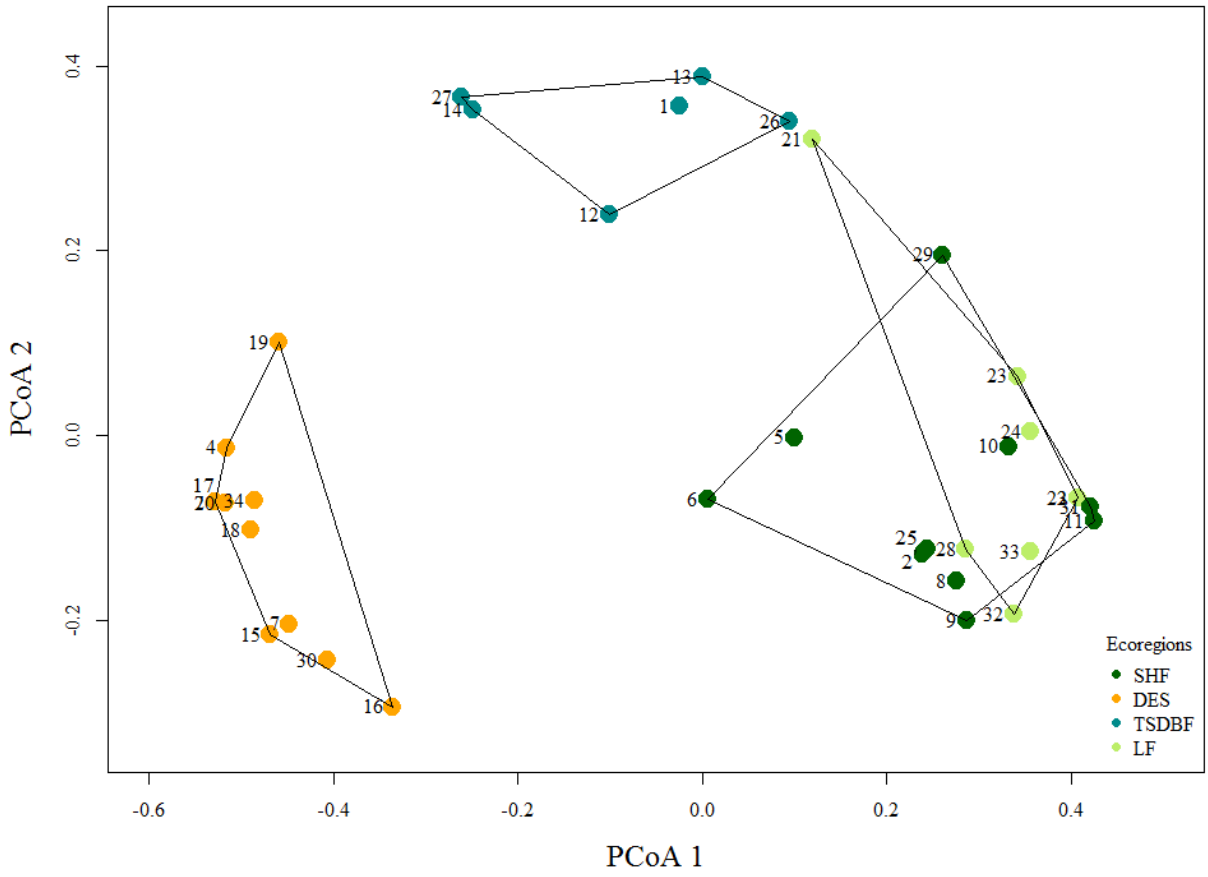


Figure 3.5. Principal Coordinate Analysis (PCoA) plot of the Jaccard index of compositional similarities by site in Madagascar's primate communities. Numbers indicate site numbers, shown in Table A.1. SHF, subhumid forests; DES, desert and xeric shrublands; TSDBF, tropical and subtropical dry broadleaf forests; LF, lowland forests.

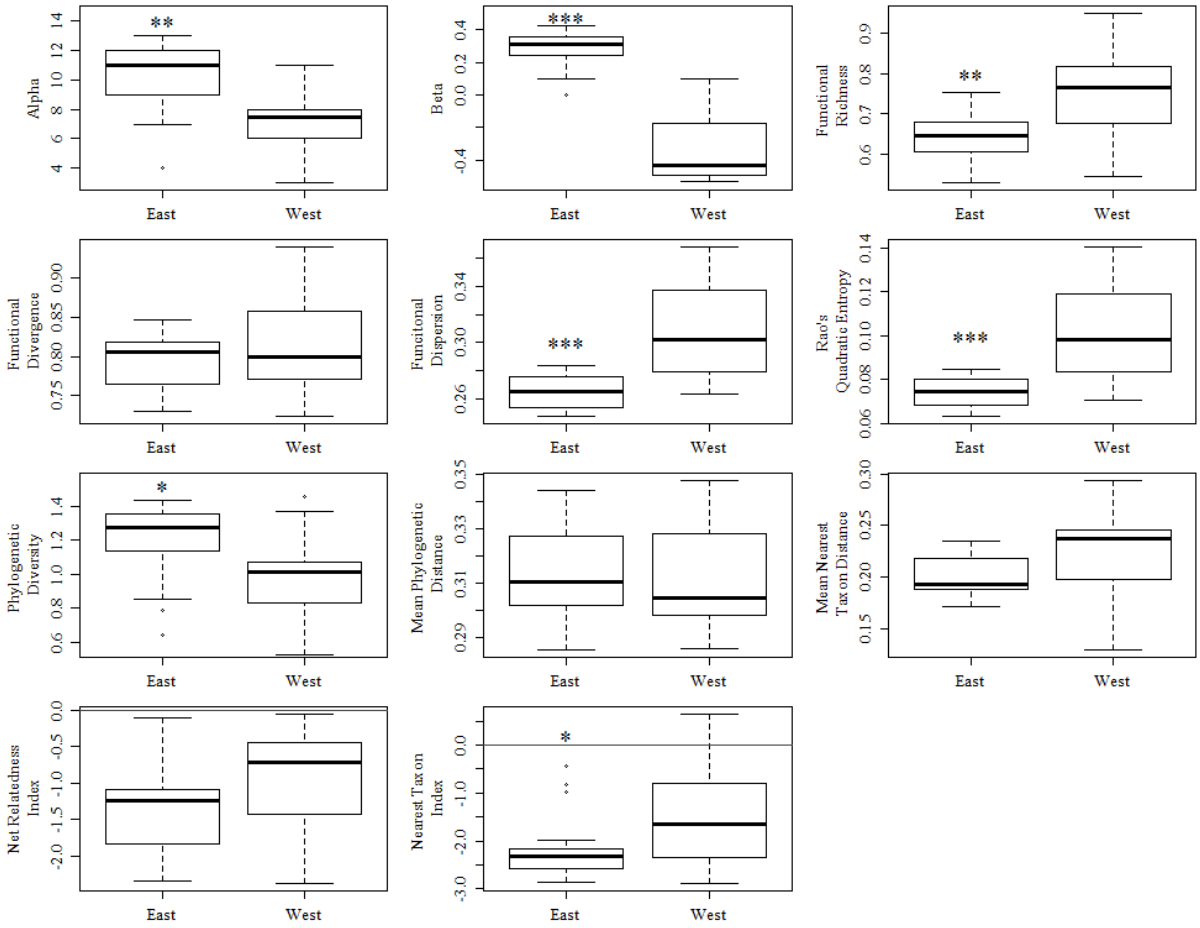


Figure 3.6. Boxplots of primate community diversity (y-axis) in Madagascar across study sites in the east and the west (x-axis). Significant differences between eastern and western Madagascar (t-test) are indicated by asterisks: $p < 0.001$***, $p < 0.01$**, $p < 0.05$*. A horizontal line is used to emphasize the zero line. Abbreviations: TSDBF, tropical and subtropical dry broadleaf forests; DES, desert and xeric shrublands; SHF, subhumid forests; LH, lowland forests.

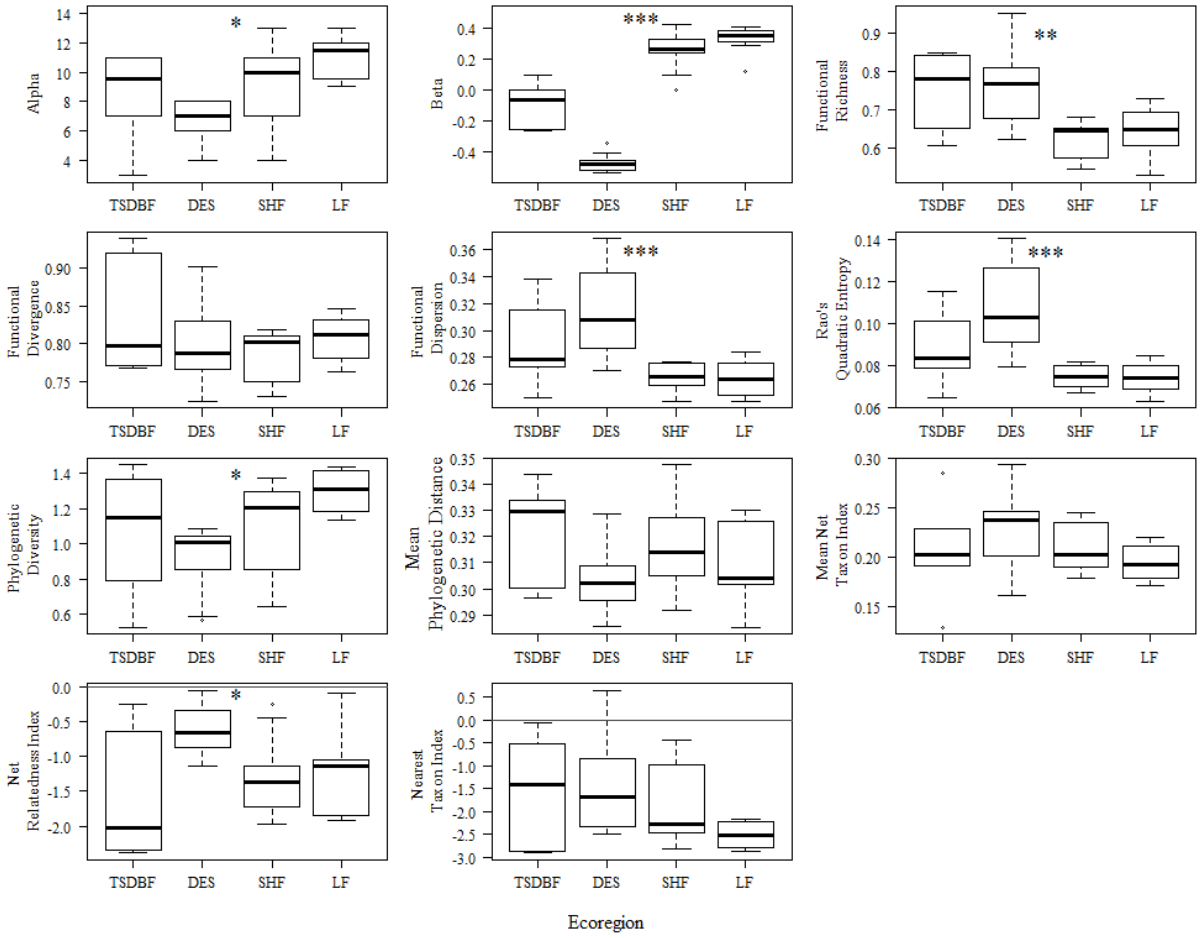


Figure 3.7. Boxplots of primate community diversity (y-axis) in Madagascar across ecoregions (x-axis). Significant differences between ecoregions (ANOVA) are indicated by asterisks: $p < 0.001$***, $p < 0.01$**, $p < 0.05$*. A horizontal line is used to emphasize the zero line. Abbreviations: TSDBF, tropical and subtropical dry broadleaf forests; DES, desert and xeric shrublands; SHF, subhumid forests; LH, lowland forest.

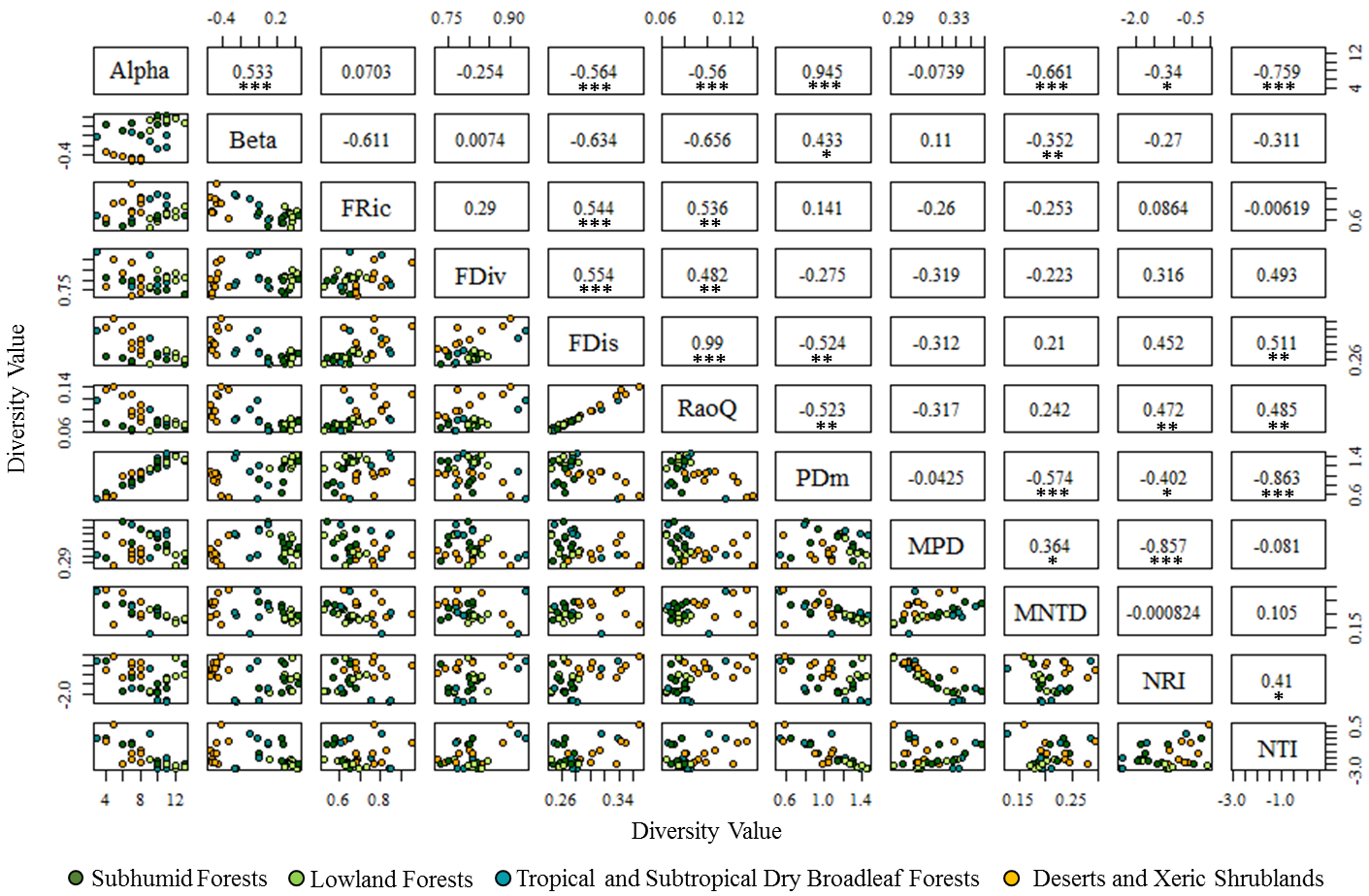


Figure 3.8. Correlation matrix of diversity measures for 34 primate communities in Madagascar. Points are coloured by ecoregion type. Pearson correlation coefficients (r) are provided in upper right of matrix. Significant correlations are denoted by asterisks: $p \leq 0.05$*, $p \leq 0.01$**, $p \leq 0.001$***. Abbreviations: FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index.

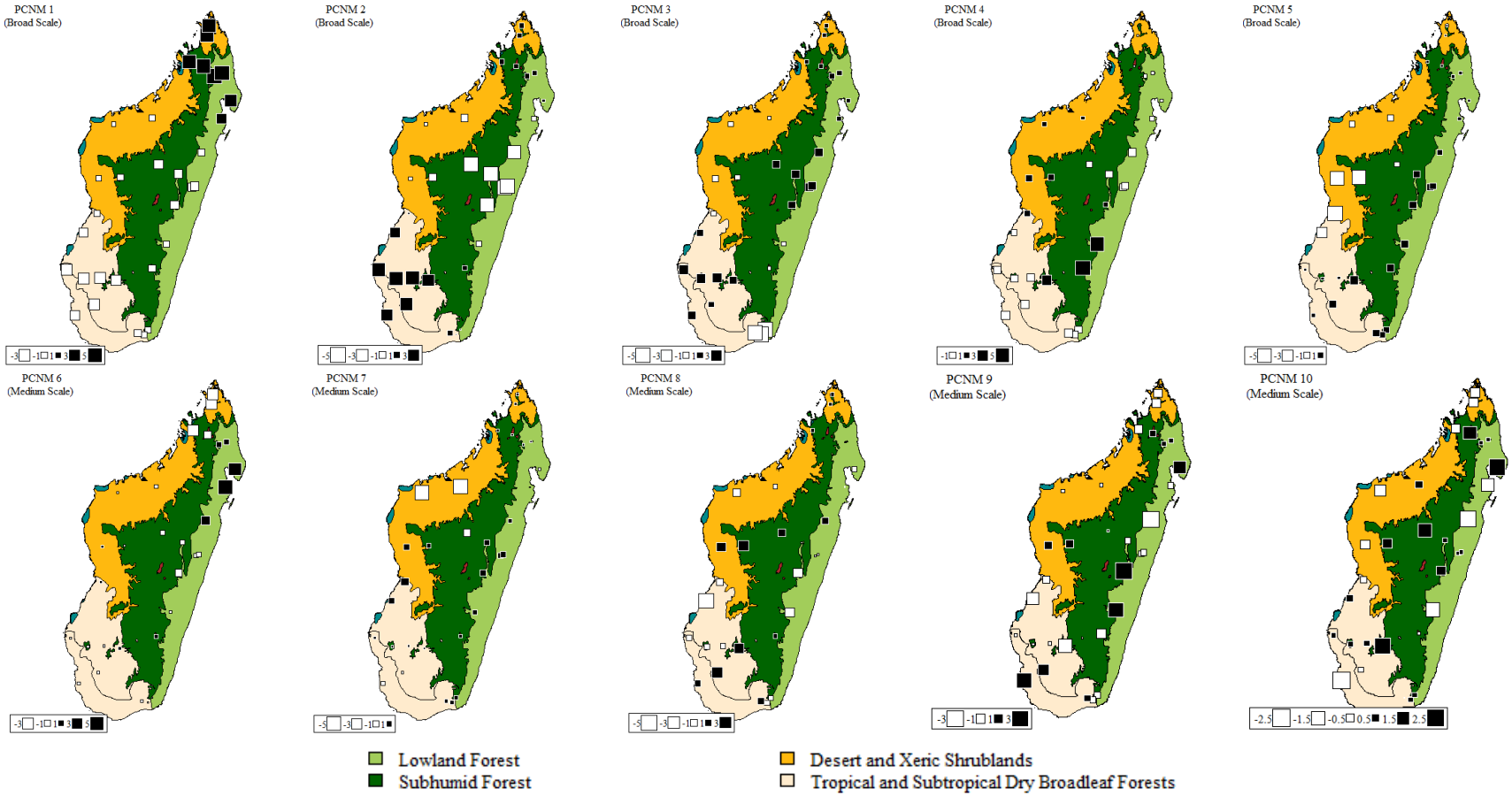


Figure 3.9. The Principal Coordinate of Neighbour Matrices (PCNM) variables with positive spatial correlation used in the PCNM analysis. PCNMs 1-5 depicted broad spatial scales and PCNMs 6-10 depicted medium spatial scales. The squares of similar size and colour represent sites with shared spatial scales. Filled squares: positive eigenvalues; empty squares: negative eigenvalues

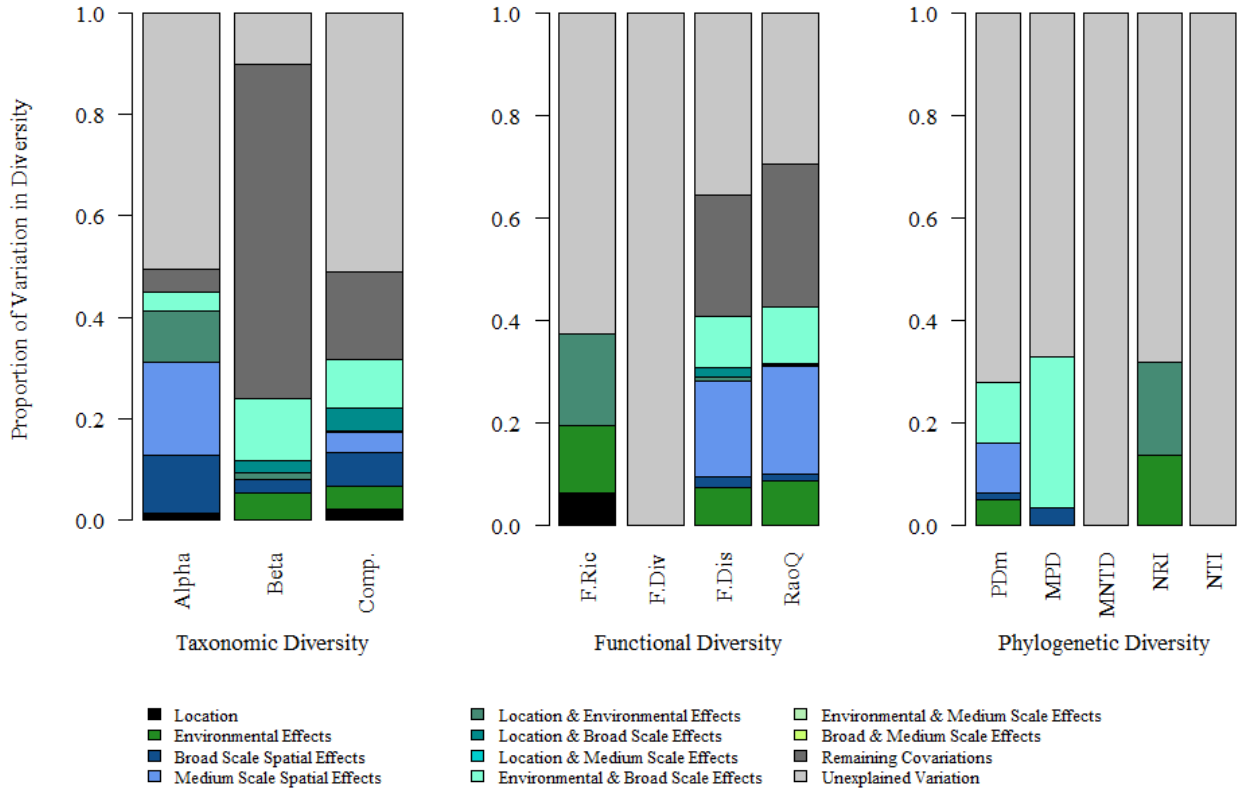


Figure 3.10. Percentage of variation in nondetrended taxonomic, functional and phylogenetic diversity explained by location, environmental, spatial and biogeographic variables. The most complete models are described here, i.e. models with the largest set of significant forward selected variables. Measures of diversity for which there are no coloured bars had no forward selected variables to include in variation partitioning. The amount of undescribed variation is a measure of model fit. Abbreviations: α, alpha diversity; β, beta diversity; FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index

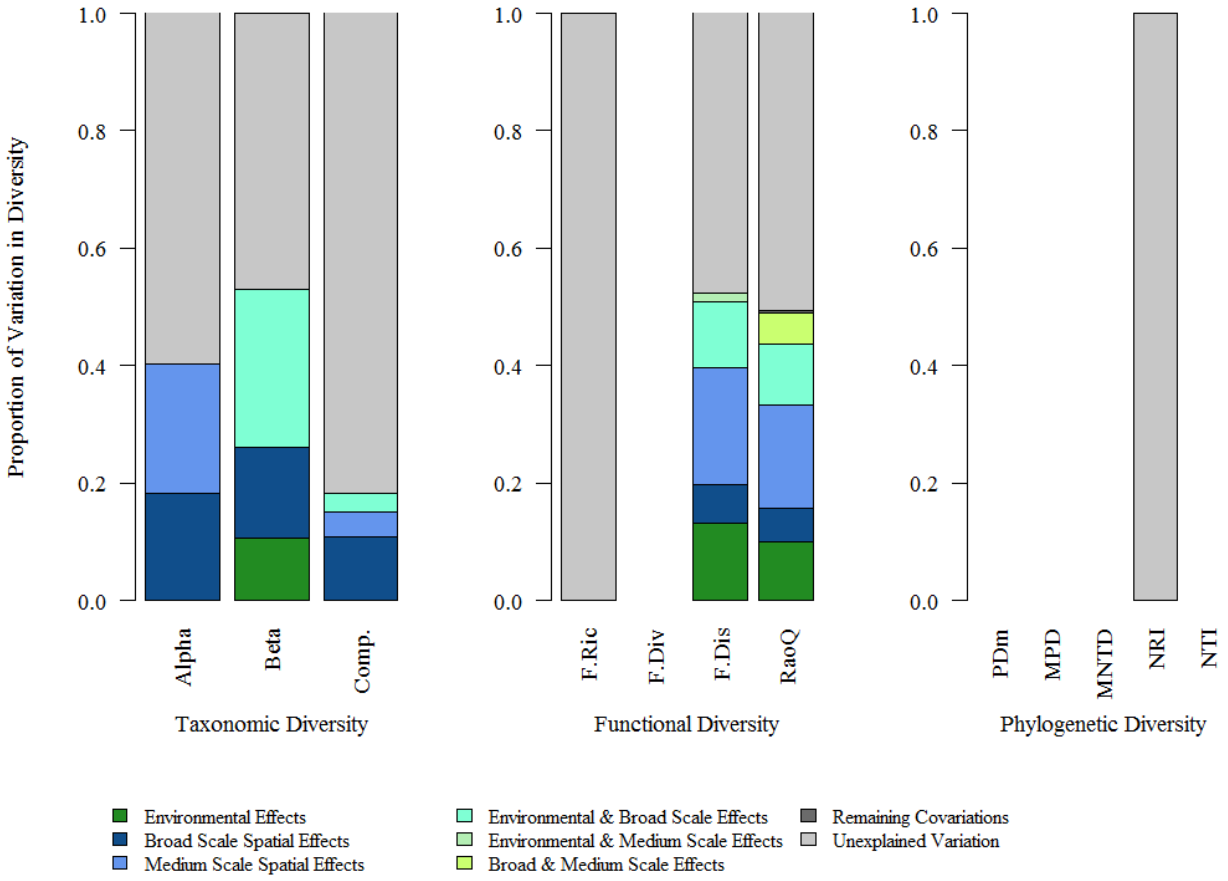


Figure 3.11. Percentage of variation in detrended taxonomic, functional and phylogenetic diversity explained by environmental, spatial and biogeographic variables. The most complete models are described here, i.e. models with the largest set of significant forward selected variables. Measures of diversity for which there are no coloured bars had no forward selected variables to include in variation partitioning. The amount of undescribed variation is a measure of model fit. Abbreviations: α, alpha diversity; β, beta diversity; FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index.

Chapter 4: Convergent Patterns of Diversity and Community Assembly in Shared Ecoregions: A comparison of mammal community assembly in Madagascar and Australia

INTRODUCTION

The assembly of mammal communities has been attributed to a combination of three different types of processes: (1) deterministic, including niche-based (Chase and Leibold 2003; Chase and Myers 2011), (2) stochastic, including neutral-based (Bell 2001; Chase and Myers 2011; Chave 2004; Hubbell 2001; MacArthur and Wilson 1967; Tokeshi 1999), and (3) historical/biogeographic (Simpson 1953; Tokeshi 1999; Vences et al. 2009). Studies of community assembly have found that patterns of assembly can be cladistically, functionally, and/or regionally specific (e.g., Beaudrot and Marshall 2011; Buckley et al. 2010; Gavilanez and Stevens 2013; Kamilar 2009; Meachen and Roberts 2014; chapter 3). Consequently, investigations into the role of diversity and regional attributes that shape patterns of community assembly are still attempting to explain patterns of diversity at various spatial and temporal scales (e.g., Chase 2003; Harrison and Cornell 2008; Morlon et al. 2011; Mouchet et al. 2010; Ricklefs 2007). Furthermore, multiple measures of diversity should be employed in the study of community assembly to identify the contribution of different assembly processes to patterns of diversity (e.g., Meynard et al. 2011; Pavoine and Bonsall 2011; Stegen and Hurlbert 2011; Swenson 2011; Münkemüller et al. 2012; but see Purschke et al. 2013).

The inclusion of functional and phylogenetic diversity in studies of community assembly may imply the operation of different community assembly processes (Cadotte et al. 2011; Cornwell et al. 2006; Mayfield et al. 2005; McGill et al. 2006; Spasojevic and Suding 2012; Stubbs and Wilson 2004; Weiher et al.1998; chapter 3). Trait analyses across taxonomic groups provides insights into how environmental factors can shape

biodiversity patterns on continental, regional, and local scales (Albert et al. 2010; McGill et al. 2006; Shipley 2010). Functional diversity is thought to be largely determined by environmental sorting (Cornwell et al. 2006; Grime 2006) where a set of environmental filters (e.g., climate, disturbance) act by selecting species with shared ecological tolerances (Diaz and Cabido 2001; de Bello et al. 2005; Grime 2006). However, in Madagascar primate communities a combination of environmental sorting and dispersal limitation by distance explain patterns of functional diversity, with spatial variables accounting for more variation (chapter 3). The additional study of phylogenetic diversity can help elucidate evolutionary/ biogeographic processes (Cavender-Bares et al. 2009; Kembel 2009), and investigate the contributions of niche-based processes (competition, environmental sorting), adaptive radiations (e.g., Cardillo 2008, 2011; Cavender-Bares et al. 2009; Graham and Fine 2008; Kraft and Ackerly 2010; Webb et al. 2002), and/or spatial processes through dispersal limitation (Eiserhardt et al. 2013; Graham et al. 2009).

Island assemblages are useful study groups for understanding community assembly processes because they are discrete, bounded, and quantifiable (e.g., Cardillo and Meijaard 2010; Okie and Brown 2009; Whittaker 1998). Island assemblages are on average phylogenetically overdispersed and randomly structured (Cardillo et al. 2008). Either the assembly processes in island mammal communities are independent of phylogenetic diversity, or trait divergence in closely related species may be more common than originally supposed and has resulted in trait divergence in closely related species due to competitive exclusion and limiting similarity in these communities (cf. Cardillo et al. 2008; Cardillo 2011; Davies et al. 2008). Moreover, the link between phylogenetic and functional diversity is often implied or assumed, and an investigation of multiple diversity metrics can establish whether a functional signal in phylogenetic diversity actually exists within a clade. An analysis of functional diversity is particularly

relevant to places where phylogenetic similarity and ecological similarity are not strongly correlated (Losos et al. 2003; Losos 2008), including the primate communities of Madagascar (chapter 3). In this case, convergence in traits may be more informative than taxonomic assemblages (Losos 2008) because the assumption that closely related species are ecologically similar (Swenson 2011) is violated.

In Madagascar, primate communities are shaped by a combination of environmental filtering and dispersal limitation, but assembly processes differentially explain taxonomic, functional and phylogenetic diversity components (chapter 3). Taxonomic diversity is strongly ecoregionally shaped and both environmental sorting and dispersal limitation shaped primate diversity. Functional diversity is predominantly shaped by dispersal limitation by distance and combined environmental-spatial structuring, with a smaller contribution attributed to environmental sorting. Phylogenetic diversity is variably shaped by environmental sorting and dispersal limitation. Biogeographic dispersal barriers explain a minor proportion of variation in primate community composition and no other measure of diversity (chapter 3). Primate communities in Madagascar were phylogenetically randomly structured and a low occurrence of sympatric congeners existed (cf. Kamilar and Guidi 2010; chapter 3). Furthermore functional and phylogenetic measures of diversity were weakly correlated (chapter 3). Madagascar is characterized by high levels of species endemicity and phylogenetic distinctiveness of higher taxa (Ceballos and Brown 1995), that are unique within global diversity and assembly models (e.g., Beaudrot and Marshall 2011; Kamilar et al. 2014). However, Madagascar provides an ideal model for testing patterns of convergent evolution because Malagasy mammal species show convergent patterns with primate species from other regions, Australian possums and gliders, and European hedgehogs (reviewed in Ganzhorn et al. 2014).

The goal of this study is to test whether diversity patterns and concurrent assembly processes are convergent for mammal assemblages in regions with similar biogeographic and evolutionary histories. Studies of diversity across multiple regions, such as islands, allow a testing of the generality of hypotheses regarding how communities are structured. Madagascar and Australia are therefore model ecosystems for comparison, and are also both characterized by long histories of independent radiation in similar biophysical environments and shared ancestral Gondwanaland biota (Ezcurra and Agnolin 2012; Jokat et al. 2003; Reeves and de Wit 2000). Both regions' extant, nonvolant mammal populations are the result of independent and discrete colonization events (cf. Archer et al. 1999; Jansa et al. 1999; Kay and Hoekstra 2008; Olson and Goodman 2003; Weyeneth et al. 2011; Woodburne and Case 1996; Yoder et al. 1996, 2003) with long periods of isolation, which have resulted in unique assemblages of species (Fooden 1972; Williams et al. 1996; Woodburne and Case 1996; Yoder et al. 2003). Consequently, Australia and Madagascar have vertebrate assemblages that are the most phylogenetically distinct globally (Holt et al. 2013, cf. Kreft and Jetz 2013).

The modern distribution patterns of arboreal mammals in Australia and Madagascar suggest that the first arboreal mammals may have had to compete with similar species, and the lemurs of Madagascar and the possums and gliders of Australia have converged on similar dietary niches (Smith and Ganzhorn 1996). *Daubentonia madagascariensis* in Madagascar and *Dactylopsila* spp. in Australia both have specialized third fingers for extracting grubs and fill the woodpecker niche in their respective habitats (Ganzhorn et al. 2014). In addition, both regions have extensive tropical evergreen rainforests in high rainfall eastern environments and seasonally dry, deciduous rainforest in the northwest of similar climate and floristic structure (Olson et al. 2001; Smith and Ganzhorn 1996, Table 4.1). However, the semi-arid environments of

both countries support endemic, floristically, and structurally unique vegetation (Olson et al. 2001; Smith and Ganzhorn 1996; Table 4.1). Consequently, Madagascar and Australia provide ideal areas to test for convergent patterns of community assembly process between areas with similar biogeographic histories, and yet shared and nonshared habitat types (ecoregions). In comparison to patterns of phylogenetic and functional diversity in temperate mammal communities, tropical mammal communities (including Madagascar and Australia) contain more functionally similar species than those present in temperate regions (Safi et al. 2011).

I investigate convergent patterns of diversity and community assembly in Madagascar and Australia because mammal taxa from these two regions evolved within similar evolutionary and biogeographic histories but have different complements of species. Ecoregions describe areas of similar floristic structure with similar climatic features (Olson et al. 2001). In addition, Malagasy and Australian arboreal mammal species show patterns of functional convergence (Smith and Ganzhorn 1996). Consequently, the objectives of this study are to identify to what extent patterns of nonvolant mammal taxonomic, functional and phylogenetic diversity and assembly vary within and between ecoregions, and within and between Madagascar and Australia. I use a similar analytical approach to chapter 3, and calculate 12 measures of taxonomic, functional, and phylogenetic diversity (Table 3.1) to describe nonvolant and arboreal mammal communities in Madagascar and Australia. I investigate intraregional (ecoregions within Madagascar and Australia), regional (within Madagascar and Australia) and inter-regional patterns (between Madagascar and Australia) in taxonomic, functional and phylogenetic diversity. I also partition the explained variation for each diversity measure due to environmental variables (testing the contribution of environmental sorting), spatial variables (constructed with principal coordinates of

neighbour matrices and testing the contribution of dispersal limitation), and biogeographic variables (measured with dispersal distance ratios; chapter 2). The hypotheses provided below on expected assembly patterns are based on the assumption of convergent patterns in diversity between Madagascar and Australia (Smith and Ganzhorn 1996). Similarly, I hypothesize that shared ecoregions host similar patterns of diversity due to homologous adaptations to similar environments (Olson et al. 2001; Safi et al. 2011). Specific metric-level predictions for each assembly process are provided in Table 3.2.

Hypothesis 1: Patterns of nonvolant mammal and arboreal mammal diversity in Madagascar and Australia are similar in shared ecoregions.

Prediction 1.1: Nonvolant mammal community and arboreal mammal community taxonomic, functional, and phylogenetic diversity values are similar in shared ecoregions (tropical and subtropical moist broadleaf forests, and deserts and xeric shrublands) in Australia and Madagascar.

Prediction 1.2: Nonvolant mammal community and arboreal mammal community taxonomic, functional, and phylogenetic diversity values are significantly different in nonshared ecoregions in Australia and Madagascar.

Prediction 1.3: Taxonomic, functional, and phylogenetic diversity values are more similar for arboreal mammal communities than for nonvolant mammal communities in shared ecoregions (tropical and subtropical moist broadleaf forests, and deserts and xeric shrublands) of Australia and Madagascar.

The taxonomic diversity of Malagasy primate communities is shaped by environmental sorting and dispersal limitation by distance (Kamilar 2009; Beaudrot and Marshall 2011; chapter 2 and 3), and dispersal around biogeographic barriers does not explain patterns of community composition (chapter 2 and 3). If environmental sorting

has shaped patterns of nonvolant mammal taxonomic diversity then diversity values will correlate with environmental variables. Similar taxonomic diversity values will be present in environmentally similar sites and vice versa (Chase 2003, 2007; Chase and Myers 2011). If dispersal limitation by distance has shaped patterns of primate taxonomic diversity then diversity values will correlate with geographic distance between sites. Values will be similar in sites that are close together and vice versa (Hubbel 2001; Loreau and Mouquet 1999; Mouquet and Loreau 2003).

Hypothesis 2: Nonvolant mammal community and arboreal mammal community taxonomic diversity is shaped by environmental sorting and dispersal limitation by distance.

Prediction 2.1: The taxonomic diversity values of nonvolant and arboreal mammal communities in Madagascar and Australia correlate with both environmental variables and the distance between sites. Similar taxonomic diversity values are found in sites that are ecologically similar and geographically close together.

Prediction 2.2: Environmental (environmental effects) and spatial variables (spatial effects) explain the greatest proportions of variation in nonvolant and arboreal mammal community taxonomic diversity measures in Madagascar and Australia.

Environmental sorting is thought to shape functional diversity (Cornwell et al. 2006; Grime 2006). However, chapter 2 showed that spatial variables (modelling dispersal limitation) variably influence arboreal and terrestrial mammal communities in Madagascar. Furthermore, in chapter 3 the functional diversity of Malagasy primate communities was more strongly shaped by spatial variables than by environmental variables, although covariation between spatial and environmental effects explained large amounts of variation. Consequently, in regions with high ecoregional variation and spatial structuring of the environment, functional diversity is shaped by both geographic

distances between sites and environmental sorting. In this study, I use the same suite of eight traits as in chapter 3. Consequently, patterns of functional diversity are expected to be strongly correlated with environmental conditions (Cornwell et al. 2006; de Bello et al. 2005; Diaz et al. 1998; Diaz and Cabido 2001; Grime 2006; Lessard et al. 2012, chapter 3), and spatial variables due to strong ecoregional effects in both Madagascar (Muldoon and Goodman 2010; chapter 2 and 3) and Australia (cf. Mazel et al. 2014; Olson and Dinerstein 2002).

Hypothesis 3: Nonvolant mammal community and arboreal mammal community functional diversity is shaped by environmental sorting and dispersal limitation by distance.

Prediction 3.1: The functional diversity values of nonvolant mammal and arboreal mammal communities in Madagascar and Australia correlate with both environmental variables and the distance between sites. Similar functional diversity values are found in sites that are ecologically similar and geographically close together.

Prediction 3.2: Environmental (environmental effects) and spatial variables (spatial effects) explain the greatest proportions of variation in nonvolant mammal and arboreal mammal community functional diversity measures in Madagascar and Australia.

Patterns of phylogenetic diversity may reflect the deterministic process of environmental sorting and competition, biogeographic processes (CavenderBares et al. 2009; Kembel 2009), and/or spatial processes through dispersal limitation (Eiserhardt et al. 2013; Graham et al. 2009). In Madagascar, primate communities are randomly phylogenetically structured with a tendency to overdispersion (Kamilar and Guidi 2010; chapter 3). Phylogenetic diversity of Malagasy primate communities is variably shaped by assembly processes and not consistently predicted across measures (chapter 3). Furthermore, phylogenetic and functional diversity measures in Malagasy primates are

weakly correlated (chapter 3) and convergence in traits on similar environments appears to be the result of adaptive radiations in lemurs (Godfrey et al. 1997, 1999). Biogeographic barriers, indicated with a measure of site isolation, did not explain patterns in Malagasy primate phylogenetic diversity. Observed patterns of overdispersion are consequently hypothesized to be the result of environmental sorting, and phylogenetic patterns of overdispersion have been found in Malagasy and Australian nonvolant mammal communities (Cardillo et al. 2008).

Hypothesis 4: Nonvolant mammal community and arboreal mammal community phylogenetic diversity is shaped by environmental sorting.

Prediction 4.1: The phylogenetic diversity values of nonvolant mammal and arboreal mammal communities in Madagascar and Australia correlate with environmental variables. Similar phylogenetic diversity values are found in sites that are ecologically similar.

Prediction 4.2: Environmental (environmental effects) explain the greatest proportions of variation in nonvolant mammal and arboreal mammal community phylogenetic diversity measures in Madagascar and Australia.

METHODS

Data Collection and Preparation

Data were collected for 34 protected areas in Madagascar and 51 protected areas in Australia within shared (DES and TSMBF) and nonshared ecoregions (TSDBF, TBMF, TGSS, TSGSS, MWFS), as classified by Olson et al. (2001, Table 4.1, Figure 4.1). Sampling in Australia was biased to the east due to the limited availability of mammal species occurrence lists for the Northern Territory, Western Australia and South Australia states. Tasmania was excluded from the dataset search because it is not attached

to Australia's mainland. For each protected area, the area in km^2 encompassed by the protected area boundaries was calculated from shapefiles. The year protection began, i.e. when the protected area was gazetted, was collected from published sources (Table A.3 and A.4). Data describing mammal communities in the Mangrove ecoregion of Madagascar and Australia were not available.

Mammal community composition was assessed by compiling occurrence data for species from published sources following Mittermeier et al.'s (2010) taxonomy for primates and Wilson and Reeder's (2005) taxonomy for nonprimates. I only used confirmed sighting data collected from scientific surveys, government reports or long-term field studies (Table A.1 and A.2). Taxonomic identifications were assigned to the species level. An ecological community was defined as all the nonvolant mammal species that potentially interact within a single patch or local area of habitat (Chase and Leibold 2003; Emerson and Gillespie 2008; Holyoak et al. 2005). Nonindigenous or domesticated species were excluded from species lists. Communities were only included in the analysis if they comprised at least five different species to avoid misinterpreting the large number of ties between observed and null communities when calculating phylogenetic diversity metrics (Webb et al. 2008). Occurrence data was compiled for confirmed species sightings only, and For each species, data on the same eight traits were obtained from the literature. I chose mammal traits that are documented to reflect ecologically relevant adaptations that indicate resource use and niche separation (Table A.5, *sensu* chapter 3). These traits included adult body mass, substrate type, feeding guild, trophic level, locomotion, activity period, habitat specificity and torpor. I further divided community species lists to include only arboreal species, or species that are both arboreal and terrestrial based on the substrate type trait. Due to this division, Australia had only 30

sites included in the arboreal analysis (Table A.2), to ensure communities had five or more species present.

Diversity Measures

Taxonomic diversity

Taxonomic diversity was measured in three ways: alpha (α) diversity (a.k.a. species richness), community composition, and beta (β) diversity (Table 3.1). Prior to analysis, community composition matrices (species × site) were Hellinger transformed to allow the use of RDA without considering the common absence of the species as a resemblance between communities (Legendre and Gallagher 2001). The Jaccard index (Jaccard 1901) was used to measure β-diversity (Table 3.1). Prior to analysis a principal coordinates analysis (PCoA) with Lingoes' correction (Lingoes 1971) for negative eigenvalues was used to describe the Jaccard dissimilarities between sites in two-dimensional space. The PCoA axes of the Jaccard index with eigenvalues of greater than one were retained for analysis, and are hereafter referred to as β. Taxonomic measures of diversity were calculated using the "vegan" (Oksanen et al. 2013) package in R (R Core Team 2014).

Functional diversity

Functional diversity of traits was measured with four complementary measures that measure different and important components of functional variation that should be considered in analysis (Laliberté and Legendre 2010; Mouchet et al. 2010): functional richness (FRic), functional divergence (FDiv), functional dispersion (FDis), and Rao's quadratic entropy (RaoQ; Table 3.1). The traits used to calculate functional diversity metrics consisted of both continuous and categorical variables (Table A.5), so the Gower method was used to calculate the distance matrix and all traits scores were standardized

to have a range of 0–1 (Gower 1971; Laliberté and Legendre 2010; Laliberté and Shipley 2011). All functional diversity measures were calculated using the 'FD' package in R (Laliberté and Legendre 2010; Laliberté and Shipley 2011). Due to the variation in availability of trait data for certain species (Table A.6 and A.9), some species had no trait values for certain traits. Trait values were not extrapolated for these species based on phylogenetic relatedness or averaging to avoid creating a false functional signal in the phylogenetic data that could not be reliably established. Torpor as a trait had the most missing values and functional diversity metrics were therefore calculated with and without torpor values. Values had a very high linear correlation ($r > 0.8$) with or without torpor, consequently, the results reported here include torpor in the functional diversity calculations.

Phylogenetic diversity

Phylogenetic diversity was calculated from the Bininda-Emonds et al. (2007) phylogeny for mammals (not including primates), and the Arnold et al. (2010) phylogeny for primates (Figure 4.2.A-D). The Bininda-Emonds et al. (2007) tree was trimmed to include only species in this study, resulting in 23 missing Malagasy species (not including primates; Table A.7) and 9 missing Australian species (Table A.8). As in chapter 3, the Arnold et al. (2010) tree was trimmed using the GenBank taxonomy, containing 56 of the 70 primate species included in this study (Table A.7). For Madagascar's mammal communities the phylogenetic tree of primates within the Beninda-Emonds et al. (2007) phylogeny was replaced with the more recent Arnold et al. (2010) primate phylogeny using "bind.tree" in the "ape" package in R (Paradis et al. 2004), and used to calculate phylogenetic diversity metrics. Five measures of phylogenetic diversity were calculated: phylogenetic diversity (PDm), mean pairwise

distance (MPD), mean nearest taxon distance (MNTD), nearest taxon index (NTI), and net relatedness index (NRI; Table 3.1). For NTI and NRI, a thousand random assemblages were generated for the null models by selecting species only from within the set of taxa present in the species pool and shuffling the distance matrix across the taxa in the community (Kembel et al. 2010). Phylogenetic measures of diversity were calculated using the "ape" (Paradis et al. 2004) and "picante" (Kembel et al. 2010) packages in R.

Effect Types

Environmental effects

Georeferenced data on environmental variables for each study site were collected from the Madagascar Digital Elevation Model (CGIAR-SRTM data aggregated to 30s; Hijmans et al. 2004), the Australia Digital Elevation Model (CGIAR-SRTM data aggregated to 30s; Hijmans et al. 2004) and the WorldClim Global Climate Database (Hijmans et al. 2005; Table 2.2). Mean values were calculated for each environmental variable within the protected area boundaries. Environmental variables were tested for significant autocorrelations (*sensu* Beaudrot and Marshall 2011) using Pearson's product-moment correlation coefficient. To minimize the over-fitting of models due to highly correlated environmental variables, variables were included in the analysis only if they had a correlation of less than 0.8 and documented influences on mammal populations (Table 2.2; Figure 2.2 and 4.3).

Spatial effects

Similar to the methods described in chapters 2 and 3, principal coordinates of neighbour matrices (PCNM) were used for the analysis of spatial effects across various spatial scales in the community composition data (Dray et al. 2006). PCNM analysis creates spatial predictors that can be directly included in regression models by computing

eigenfunctions of spatial connectivity matrices (Griffith and Peres-Neto 2006). PCNM uses a principal coordinate analysis of Euclidean distance matrix among study sites. The analysis truncates each matrix at the smallest distance between nearest neighbors that keeps all sites connected in a single network (Figures 3.3 and 4.4). The eigenvectors (PCNMs) that modeled positive spatial correlation were retained and used to represent spatial structuring in patterns of community diversity. The first PCNMs represent broad scale spatial structures, with successive PCNMs representing progressively smaller spatial scale effects (Borcard and Legendre 2002) ranging between 1400 km (broadest scale) to 26 km (smallest scale) in Madagascar and 2657 km to 13 km in Australia. Consequently, PCNMs with positive eigenvectors were evenly separated into small, medium, and broad spatial scales to reflect the spatial grain of the study sites (*sensu* García et al. 2010). The terms "small," "broad," and "medium" scales were defined relative to this particular set of study sites and were constrained by the data's resolution and spatial extent. PCNM variables were created using the R package ''PCNM'' (Legendre et al. 2010), based on geographic coordinates for each study site centroid. Geographic coordinates were calculated from the protected area boundaries (*Madagascar*: Gerber 2010; *Australia*: CAPAD 2008) in ArcGIS 10.1 (Feature to Point tool) of each site.

Biogeographic effects

Biogeographic effects were measured as an effective distance ratio for each type of biogeographic barrier considered (permanent rivers and bodies of water, elevation slope, and the island edge; Figure 4.5), as calculated in chapters 2 and 3 (Equation 2.1). Data on biogeographic dispersal barriers were extracted from digital maps of Madagascar and Australia (Hijmans et al. 2004; Lehner and Doll 2004); including permanent rivers

and bodies of water, elevation slope, and the island edge (Table 2.2). The elevation range in Australia does not extend beyond 22.5º slope increments and was therefore not included as a biogeographic barrier.

Statistical Analyses

Analyses were conducted in R 3.1.0 (R Core Team 2014). Statistical tests were considered significant at $p < 0.05$. The multivariate response of Madagascar's and Australia's nonvolant mammal communities and arboreal nonvolant mammal communities were modeled to a matrix of environmental variables, spatial variables (PCNMs) and biogeographic effective distance ratios using variation partitioning techniques. In this modeling approach the diversity metric was the response variable, and the environmental, spatial and biogeographic variable sets were the explanatory variables (Figure 4.6).

Diversity regressions, PCNM, and variation partitioning were all performed for Madagascar's and Australia's nonvolant mammal and arboreal mammal communities. Deviations from the methods presented in chapter 3 are presented here. Regional (Madagascar versus Australia) differences in diversity were tested with Mann-Whitney U tests. Ecoregional differences between Madagascar and Australia's two shared ecoregions (DES, TSMBF) were tested with ANOVA and pairwise t-tests. Because of the multiple pair-wise t-tests required, Bonferroni p-value correction and Tukey's post hoc tests were used to assess significance. Differences were counted as significant if determined significant by both tests. Principal coordinates analysis of the Jaccard similarity in nonvolant mammal communities could not be tested for significant differences between Australia and Madagascar, nor could composition because there were no shared nonvolant or arboreal mammal species in Madagascar and Australia. Furthermore,

although patterns of β-diversity were compared they are specific to each region because the eigenvalues produced from the PCoA analysis are unique to the communities and species assemblages described.

I tested the relationship between alpha diversity and protected area size using a linear model, the log-log linear model (or power model), the non-linear Arrhenius model, and the Gleason model and model fits were compared using the Aikake criterion (AIC; *sensu* chapter 3). I also tested the relationship between alpha diversity and protected area age (year protected area gazetted subtracted from 2014) with a linear regression. I included the protected area variables (area and age) in the forward selection analyses to account for their potential contribution to diversity patterns. However, I did not test the proportion of variation due to protected area variables because they are not measures of the contribution of assembly processes to shaping community diversity.

Variation partitioning was conducted in two ways for Madagascar and Australia (Figure 4.6): *Model 1*: using forward selected environmental, biogeographic, broad, and fine scale PCNMs, and including the linear trend of composition and geographic location without detrending composition (*sensu* Borcard et al. 2011); and *Model 2*: using forward selected environmental, biogeographic, broad and fine scale PCNMs with detrended community compositions if latitude or longitude were significant. Several components of variation are reported: pure effects where the variation was attributable to a single source (e.g., pure environmental effects), total effects where the total amount of variation is attributable to a source and its covariations with other variables (e.g., total environmental effects), and shared spatial-environmental effects (the shared variation of environmental and spatial effects).

RESULTS

Regional and Ecoregional Diversity Patterns

Patterns in diversity were variable across both Australia and Madagascar at both levels of community grouping (i.e., all nonvolant mammals and arboreal mammals). Significant differences in diversity existed between Madagascar and Australia for all nonvolant mammal communities in α-diversity (Figure 4.7.A), all measures of functional diversity (FRic, FDiv, FDis, and RaoQ; Figure 4.8.A), and phylogenetic diversity (MPD, MNTD, NRI, and NTI; Figure 4.9.A). Regionally, Malagasy nonvolant mammal communities had higher species richness, lower functional richness, and smaller ranges of phylogenetic diversity values. However, measures of trait divergence (FDiv) and dispersion (FDis and RaoQ) were higher in Madagascar than Australia. NRI (p value $\bar{x} \pm SD = 0.367 \pm 0.308$) and NTI ($p$ value $\bar{x} \pm SD = 0.641 \pm 0.271$) values for Australian nonvolant mammal communities were not significant over 1000 simulations overall. However, five Australian nonvolant mammal community sites had significant NRI values, and two sites had significant NTI values. No significant NTI or NRI values were observed in any Malagasy community sites. The absence of significant NTI and NRI in Malagasy nonvolant mammal communities and the presence of significant and positive NRI and NTI values for some sites in Australia indicate that communities are phylogenetically clustered, or composed of species that are more closely related than expected by chance in Australia and randomly structured in Madagascar (Table 3.1). Higher MPD and MNTD values were also found in Australia indicating higher levels of phylogenetic diversification and phylogenetic overdispersion in comparison to Madagascar's nonvolant mammal communities (Table 3.1, Figure 4.9A).

Arboreal mammal communities were significantly different in α-diversity, FRic, FDis, RaoQ, and NTI between Madagascar and Australia (Figures 4.10.A-4.12.A).

Malagasy arboreal mammal communities had higher species richness, lower functional richness, but phylogenetically structured communities similar to Australia. Measures of trait dispersion (FDis and RaoQ) were higher in Madagascar than Australia, similar to the patterns found for nonvolant mammal communities. Of the arboreal mammal community sites in Australia, two had significant NRI values and one had a significant NTI value. No significant NTI or NRI values were observed in any Malagasy community sites. The presence of significant and positive NRI and NTI values for some sites in Australia indicate that some communities were phylogenetically clustered, but the majority of communities were randomly structured. The only significantly different phylogenetic diversity measure between Madagascar and Australia was NTI, indicating that Australia had more phylogenetic clustering at the tips of community phylogenies than Madagascar, but phylogeny-wide patterns (as measured by NRI) were random.

Across ecoregions, distinct patterns in diversity were present for nonvolant mammals (Figure 4.7.B-4.9.B, 4.13). Nonvolant mammal α-diversity was highest in the TSMBF ($\bar{x}$ = 31.8) ecoregion of Madagascar and highest in the TBMF ($\bar{x}$ = 27.0) ecoregion of Australia (Figure 4.7.B). Beta diversity values, described by the first PCoA axis, were highest in the DES ecoregion for both Madagascar ($\bar{x}$ = 0.43) and Australia ($\bar{x}$ = 0.46) and lowest in the TSMBF ($\bar{x}$ = -0.20) ecoregion of Madagascar and the TBMF ($\bar{x}$ = -0.27) ecoregion of Australia. The FRic values for Madagascar were very low across ecoregions ($\bar{x}$ = 0.03) and higher ($\bar{x}$ = 0.19) in Australia with the highest values observed in the TBMF ecoregion (Figure 4.8.B). FDiv was highest in the DES ecoregion of Madagascar ($\bar{x}$ = 0.88) and had the highest mean value in the DES ecoregion of Australia ($\bar{x}$ = 0.90). FDis and RaoQ (both functional dispersion measures) were similarly structured across ecoregions with highest values observed in DES of Madagascar ($\bar{x}$ = 0.33; $\bar{x}$ = 0.12, respectively) and TGSS of Australia ($\bar{x}$ = 0.31; $\bar{x}$ = 0.10, respectively).

PDm was highest in the TSMBF ecoregion of Madagascar ($\bar{x}$ = 917.69) and the TBMF ecoregion of Australia ($\bar{x}$ = 999.56), although the highest PDm value in the TSMBF ecoregion was comparable to that observed in the TBMF (Figure 4.9.B. The highest MPD values were observed in the TSMBF ecoregion of Madagascar ($\bar{x}$ = 158.94), and the DES ecoregion of Australia ($\bar{x}$ = 218.64). For MNTD the highest values were observed in the DES ecoregion of Madagascar ($\bar{x}$ = 67.0) and the TGSS ecoregion of Australia ($\bar{x}$ = 67.4). NRI was highest in the TSDBF ecoregion of Madagascar ($\bar{x}$ = -0.94) and the TBMF ecoregion of Australia ($\bar{x}$ = 1.19). Finally, NTI for nonvolant mammal communities was highest for the TSDBF ecoregion of Madagascar ($\bar{x}$ = -0.51) and the TSMBF ecoregion of Australia ($\bar{x}$ = -0.32).

Compositional patterns of nonvolant mammal communities, indicated by PCoA plots of the Jaccard index of compositional similarity, showed ecoregional differences within Madagascar and Australia (Figure 4.13). The values of the Jaccard index cannot be compared directly between Madagascar and Australia, because they are within-region measures, however the clustering of values within regions can be broadly compared. Madagascar's nonvolant mammal communities were compositionally similar within ecoregions, however site 21 (Monangarivo) and site 26 (Montagne d'Ambre) approached each other in PCoA space, and were more similar to each other than to the other sites in their ecoregion cluster. Monangarivo is on the northwestern side of the island, in contrast to the majority of TSMBF sites and borders the TSDBF ecoregion, contributing to its high similarity with TSDBF nonvolant mammal communities, including that of Montagne d'Ambre. In Australia, nonvolant mammal community composition was also ecoregionally clustered with a lot of overlap for the TSGSS, TGSS and MWFS ecoregions. In addition, site 11 (Carnarvon in TSGSS) and site 44 (Torrington in TBMF) appear to cluster better with each other's ecoregion than their own (Figure 4.13).

Arboreal mammal communities in Australia and Madagascar were also ecoregionally variable (Figures 4.10.B-4.12.B, 4.14). The highest arboreal community α-diversity was found in the TSMBF ecoregion of Madagascar ($\bar{x}$ = 15.6) and the TBMF ecoregion of Australia ($\bar{x}$ = 10.3, Figure 4.10.B). Beta diversity was highest in the DES ecoregion of Madagascar ($\bar{x}$ = 0.46) and the TSMBF ecoregion of Australia ($\bar{x}$ = 0.47). FRic was highest in the TSMBF ecoregion of Madagascar ($\bar{x}$ = 0.09) and the TBMF ecoregion of Australia ($\bar{x}$ = 0.22; Figure 4.11.B). FDiv presented the same pattern as FRic, however the highest median values of FDiv were observed in the DES ecoregion of Madagascar ($\bar{x}$ = 0.88). FDis and RaoQ were similar with the highest values observed in the DES ecoregion of Madagascar ($\bar{x}$ = 0.34; $\bar{x}$ = 0.12, respectively) and the TGSS ecoregion of Australia ($\bar{x}$ = 0.28; $\bar{x}$ = 0.08, Figure 4.11.B). PDm was highest in the TSMBF of Madagascar ($\bar{x}$ = 561.04) and the TBMF of Australia ($\bar{x}$ = 537.55), meaning their communities had the highest combined branch lengths and deeper phylogenetic histories than the lowest values observed in the DES ecoregion of Madagascar ($\bar{x}$ = 503.58) and the TSMBF ecoregion of Australia ($\bar{x}$ = 480.92, Figure 4.12.B). The MPD was highest in the TSDBF ecoregion of Madagascar ($\bar{x}$ = 127.21) and the TSMBF ecoregion of Australia ($\bar{x}$ = 159.69), where the highest value was twice the average reported in Madagascar. The highest MNTD values in Madagascar were in the DES ecoregion ($\bar{x}$ = 88.71) and in the TSMBF ecoregion of Australia ($\bar{x}$ = 67.11), with the highest median value observed in the TGSS ($\bar{x}$ = 89.2). NRI was highest in the TSDBF ecoregion of Madagascar ($\bar{x}$ = 0.68) and had more negative values than in other ecoregions. The highest positive NRI values in Australia were in the TBMF ecoregion ($\bar{x}$ = 0.95); the lowest values were mostly negative (in contrast to Madagascar) and were found in the TSMBF ecoregion ($\bar{x}$ = -0.58). NTI in Madagascar was highest in the

TSDBF ecoregion ($\bar{x}$ = -0.42) and in the TBMF ecoregion of Australia ($\bar{x}$ = 0.17, Figure 4.12.B).

Arboreal mammal community compositional patterns, indicated by PCoA plots of the Jaccard index of compositional similarity, showed ecoregional differences within Madagascar and Australia (Figure 4.14). Madagascar's arboreal mammal communities were compositionally similar within ecoregions, however site 26 (Montagne d'Ambre) more closely grouped with the composition of TSMBF communities than TSDBF communities. In Australia, nonvolant mammal community composition was also ecoregionally clustered with distinct areas of PCoA space occupied by communities from TBMF, TSGSS and TSMBF ecoregions (Figure 4.14).

Comparing diversity measures between shared ecoregions in Madagascar and Australia for nonvolant mammal communities revealed nonsignificant differences in α, β, FDiv, PDm, MNTD, NRI, and NTI in the DES ecoregion and for FRic in the TSMBF ecoregion (Table 4.2). No arboreal mammal communities in the DES ecoregion in Australia had more than five species; consequently, a comparison of diversity between shared ecoregions was not calculated. Nonsignificant differences in diversity between TSMBF sites in Madagascar and Australia were observed for FRic and MNTD (Table 4.2).

Diversity Regressions

Diversity measures for both Malagasy and Australian nonvolant mammal and arboreal mammal communities had varying relationships with species richness (α-diversity; Table 4.3; Figure 4.15.A-D). Within Madagascar, significant and strong (Adj. $R^2 > 0.5$) relationships exist between nonvolant mammal species richness and β-diversity (Adj. R^2 = 0.741), FRic (Adj. R^2 = 0.685), PDm (Adj. R^2 = 0.920), MNTD (Adj. R^2 =

0.610), and NRI (Adj. R^2 = 0.527). For arboreal mammals significant and strong relationships between diversity measures and species richness existed for FRic (Adj. R^2 = 0.639), PDm (Adj. R^2 = 0.564) and MNTD (Adj. R^2 = 0.596). Within Australian nonvolant mammal communities strong significant relationships existed between species richness and β-diversity (Adj. R^2 = 0.613), FRic (Adj. R^2 = 0.912) and PDm (Adj. R^2 = 0.909). Strong diversity relationship with species richness in Australian arboreal mammal communities were with FRic (Adj. R^2 = 0.818) and PDm (Adj. R^2 = 0.732; Table 4.3).

Comparisons of correlations between diversity measures revealed weak overall patterns of diversity metrics with each other. In Malagasy nonvolant mammal communities strong correlations existed for α × β, α × FRic, α × PDm, β × PDm, β × MNTD, FRic × RaoQ, FDis × RaoQ, and MPD × NRI (Figure 4.15.A). Functional and phylogenetic measures of diversity were overall weakly correlated. PDm had a strong relationship with FRic (r = 0.808) and FDis had a strong relationship with RaoQ (r = 0.991; Figure 4.15.A). Australian nonvolant mammal communities had significant and strong correlations between α × FRic, α × PDm, β × FRic, FRic × PDm, FDis × RaoQ, and MPD × NRI (Figure 4.15.B). Overall, functional and phylogenetic diversity measures were weakly correlated. For both Madagascar and Australia, regressions between diversity measures of nonvolant mammal communities were ecoregionally dependent. Clear clustering in values exists by ecoregion for α, β and FRic diversity correlations in both regions (Figure 4.15.A and B). Patterns are less ecoregionally demarcated for FDis, RaoQ and phylogenetic diversity measures.

Arboreal mammal communities in Madagascar had strong correlations (r > |0.80|) between α × FRic, FDiv × FDis, FDiv × RaoQ, FDis × RaoQ, and MPD × NRI (Figure 4.15.C). Arboreal mammal communities in Australia had strong correlations between α and FRic and PDm, and between FDis and RaoQ, and between MPD and NRI (Figure

4.15.D). For arboreal mammal communities in both Madagascar and Australia correlations between functional and phylogenetic measures of diversity were generally weak ($r < 0.783$, Figure 4.15.C and D). Similar to the nonvolant mammal communities of Madagascar and Australia, regressions between diversity measures for arboreal mammal communities were ecoregionally dependent. Clear clustering in values existed by ecoregion for α, β and FRic diversity correlations in Madagascar (Figure 4.15.B) and for β-diversity and FDiv in Australia (Figure 4.15.D)..

Alpha diversity of nonvolant mammal communities in Madagascar and Australia were not dependent on the size of the protected area, regardless of model tested (Table 4.4). A significant relationship between α-diversity and age of the park however did exist for Australian nonvolant mammal communities ($t = -2.497$, df = 32, $p = 0.016$). However, the age distribution of national parks of Australia were divided between two time periods, with 24 of the 51 sites gazetted in 1900 and the remaining 27 sites gazetted between 1967 and 2007 (Table A.4). Once the division in gazetting time periods was accounted for no significant relationship between age and species richness existed (1900: $t = 0.0195$, $p = 0.847$; post-1900: $t = 1.697$, $p = 0.102$). Arboreal mammal community α-diversity in Madagascar was not significantly correlated with the size of the protected area in Madagascar (regardless of model; Table 4.5) or the age of the protected area ($t = -0.388$, df = 32, $p = 0.701$; Table 4.5). Species richness of Australian arboreal mammal communities, however, was significantly related to protected area size for all models tested (Table 4.5), where the log-Arrhenius model had the highest fit (AIC = 14.242). Species richness of Australian arboreal mammal communities did not have significant relationship with protected area age ($t = 0.182$, df = 32, $p = 0.857$; Table 4.5).

Environmental, Spatial and Biogeographic Effects

The range of values describing environmental effects in shared ecoregions between Madagascar and Australia varied (Table 4.6). Annual mean precipitation, precipitation seasonality, and temperature seasonality were significantly different in the DES ecoregion between Madagascar and Australia, with higher mean precipitation and precipitation seasonality observed in Madagascar, and higher temperature seasonality observed in Australia (Table 4.6). By contrast, the TSMBF ecoregion was significantly different between Madagascar and Australia for annual mean temperature, temperature seasonality and elevation, with higher annual mean temperature and temperature seasonality observed in Australia and higher elevation ranges present in Madagascar (Table 4.6).

Madagascar and Australia were comparable at broad spatial scales and variably patterned at finer spatial scales (Figures 3.7 and 4.16). As described in chapter 3, 20 PCNMs were present for the 34 study sites in Madagascar, of which 10 eigenvectors had positive spatial correlations. These 10 eigenvectors represented two spatial scales: broad (PCNMs 1–5) and medium (PCNMs 6–10) (Figure 3.7). In Australia 22 PCNMs were present, of which 13 eigenvectors had positive spatial correlations. The 13 PCNMS described broad (PCNMs 1–7) and medium (PCNMs 8–13) spatial scales (Figure 4.16). No small-scale spatial structures were positive and/or significant in Madagascar (PCNMs 10–20) or Australia (PCNMs 14–22). In Madagascar and Australia, PCNM 1 describes a latitudinal gradient between sites, differentiating the north from the south, and PCNM 2 describes a combination of a latitudinal and longitudinal division between mammal communities in the northeast and those in the southwest (Figures 3.7 and 4.16). In both Madagascar and Australia, the patterns in site scores for each PCNM vector at

progressively smaller spatial scales are more variable intra-regionally, with fewer apparent broad scale differences (Figures 3.7 and 4.16).

The biogeographic dispersal costs of travelling around biogeographic boundaries were magnified in Australia, with larger Euclidean distances between sites and higher effective distance ratios compared to those in Madagascar. The average Euclidean distance between sites for nonvolant mammal sites in Australia was almost double ($\bar{x}$ = 1056.44) the distances in Madagascar ($\bar{x}$ = 562.76 km), and less than double for Australian arboreal community sites ($\bar{x}$ = 859.09 km; Table 4.7). Biogeographic effective distance ratios accounting for the costs of traveling within island boundaries (edge) were similar for Malagasy and Australian nonvolant community sites ($\bar{x}$ = 1.06) and Australian arboreal community sites ($\bar{x}$ = 1.05; Table 4.7). However the mean effective distance ratios describing dispersal around permanent water bodies in Australia were substantially higher for nonvolant community sites ($\bar{x}$ = 1.89) and more than double for arboreal community sites ($\bar{x}$ = 2.44) than for those in Madagascar ($\bar{x}$ = 1.06; Table 4.7).

Nonvolant Mammal Communities—Linear Trends and Forward Selection of Variables

Model 1

Significant linear trends in diversity were observed in Madagascar nonvolant mammal communities for all three taxonomic measures of diversity (Table 4.8), three measures of functional diversity (FRic, FDis and RaoQ) and three measures of phylogenetic diversity (PDm, MNTD, and NRI). Longitude was common to all measures, except for FDis which had a significant relationship with Latitude (Table 4.8). These nine measures were then detrended for further analysis (model 2). For Australian nonvolant mammal communities significant linear trends in diversity were present in all three

measures of taxonomic diversity, three measures of functional diversity (FDis, FRic, and RaoQ) and four measures of phylogenetic diversity (PDm, MPD, MNTD, and NRI). Longitude was significant for all three measures of taxonomic diversity, FDis, FRic, RaoQ, PDm, MNTD, and NRI. Latitude was significant for composition, β, FDis, RaoQ, MPD, and NRI (Table 4.8).

Environmental variables were significant and forward selected for all measures of Malagasy nonvolant mammal community diversity except for FDiv and MPD. Temperature seasonality and annual precipitation were common to all three measures of taxonomic diversity, FRic, PDm, MNTD, NRI and NTI. The edge distance ratio was the only forward selected biogeographic variable for Malagasy nonvolant mammal communities when measured by composition, β, PDm, and NRI. Protected area variables (area and age) were not significant forward selected variables for any measure of Malagasy nonvolant mammal diversity (Table 4.8). The same five PCNM variables (PCNM1,2,5,4,7) were significant and forward selected for all three taxonomic diversity measures. Significant broad scale spatial effects (PCNM1-5) were present for FDis, FRic and RaoQ, and medium scale spatial effects were present for FDis and RaoQ (PCNM8). Phylogenetic diversity measures had PCNM1 common to PDm, MNTD, and NRI.

In Australia, taxonomic diversity measures all had significant environmental components, with temperature seasonality and mean annual precipitation common to all three measures (Table 4.8), as was found in Madagascar. FDis, FRic, and RaoQ had significant environmental variables forward selected with temperature seasonality common to all three measures. Phylogenetic diversity had significant environmental components in nonvolant mammal diversity when measured by PDm, MPD, NRI, and NTI. Temperature seasonality significantly described PDm, MPD and NRI. Biogeographic distance ratios were significant and forward selected for α, composition,

β, FRic, and PDm, which were all significantly influenced by the permanent water body effective distance ratio. Protected area variables were significant for α, composition, β, FDiv, FRic, MPD, and NRI, with the age of the protected area common to all seven measures. All measures of Australian nonvolant mammal diversity were significantly spatially structured, except for FDiv, MNTD and NTI. Taxonomic measures of diversity were all shaped by PCNM1 and 2. PCNM 2 (a broad scale spatial effect) was common to FRic, FDis, RaoQ, PDm and MPD (Table 4.8).

Model 2

Nine diversity measures for nonvolant mammal communities in Madagascar were detrended (α, composition, β, FRic, FDis, RaoQ, PDm, MNTD, and NRI; Table 4.9). No biogeographic or protected area variables were significant for any detrended measures of diversity. Environmental variables were forward selected for α, composition, β, FRic, and PDm. Composition, FRic and PDm had significant spatial structures once detrended (Table 4.9). Ten measures of diversity describing Australian nonvolant mammal communities were detrended (α, composition, β, FDis, FRic, RaoQ, PDm, MPD, MNTD, and NRI; Table 4.9). Environmental variables were significant for composition and β-diversity and were both described by elevation, temperature and precipitation seasonality and annual mean temperature. PDm and FDis had no forward selected variables of any kind once detrended. Biogeographic variables were not significant for any measure of detrended nonvolant mammal diversity in Australia. Protected area variables were significant for α, composition, β, FRic, and MNTD, with area common to all five measures. Spatial variables were significant for composition, β, RaoQ, MPD, and NRI (Table 4.9).

Arboreal Mammal Communities—Linear Trends and Forward Selection of Variables

Model 1

Significant linear trends in arboreal mammal diversity were present for α, composition, β, FDis, FDiv, FRic, RaoQ, and MNTD in Malagasy arboreal mammal communities (Table 4.10). Longitude was common to all three measures of taxonomic diversity and MNTD; latitude was common to all four functional diversity measures. In Australia, significant linear trends in arboreal mammal community diversity were present for composition and β, FDiv, MPD, and NTI, with latitude being common to all five measures.

Environmental variables were significant for all measures of taxonomic and functional diversity in Malagasy arboreal communities (Table 4.10). Temperature seasonality and annual precipitation shaped α, composition, β and FRic, and elevation shaped FDiv, FDis and RaoQ. Of the phylogenetic diversity measures, only MNTD was significantly shaped by an environmental variable (annual precipitation). Only arboreal community composition was significantly shaped by a biogeographic variable, the edge distance ratio. Protected area variables were only significant for PDm in Malagasy arboreal communities, with age of the protected area forward selected. Broad scale spatial variables were common to all three measures of taxonomic diversity (PCNM1, 2, 4) and PCNM1 and PCNM4 were common to three measures of functional diversity (FDis, FDiv, RaoQ). Phylogenetic measures of diversity did not share significant spatial scales, and only two measures had significant spatial components (PDm: PCNM8, 2, 7, and MNTD: PCNM4, 1, 2). In Australia, arboreal mammal communities measured by composition, β, FDiv and NRI were shaped by mean annual precipitation. Alpha, MPD, and NRI were all significantly described by mean annual temperature. Biogeographic

variables were significant for composition, β, FDiv, and NTI, which were all described by the water effective distance ratio. Protected area variables were significant for composition, β, FDiv, MPD and NRI, with age common to all five measures. Broad scale spatial variables were significant for composition, β, FDiv, MPD, and NRI, which were all shaped by PCNM1. No significant variables existed for α, FDis, FRic, RaoQ, and MNTD (Table 4.10).

Model 2

Eight measures of diversity describing arboreal mammal communities in Madagascar were detrended (α, composition, β, FRic, FDis, FDiv, RaoQ, and MNTD; Table 4.11). Only composition, β, and MNTD had significant forward selected variables once detrended. Significant environmental components existed for composition, and β-diversity. Only composition had significant spatial variables (PCNM4, 6, 2, 3). Protected area size was the only significant variable forward selected for MPD. In Australia, five measures of diversity were detrended (composition, β, FDiv, MPD, and NRI). The permanent waterbody effective distance ratio was the only significant variable forward selected for FDiv. None of the other detrended arboreal mammal community diversity measures in Australia were significantly explained by the variables tested in this study (Table 4.11).

Nonvolant Mammal Communities: Variation Partitioning

To enable effective comparisons between variation partitioning models between Madagascar and Australia and community groupings, the models including location, environmental effects, broad and medium spatial effects are explained below. Biogeographic effects were typically not included due to minor and nonsignificant

contributions to model fit (no proportion of variation greater than 1%, except for three measures of Australian arboreal diversity detailed below; Table 4.12).

Model 1

Environmental effects and spatial effects explained comparable proportions of variation in Malagasy nonvolant mammal community taxonomic diversity when measured by α-diversity (environment: 8.4%; spatial: 8.1%) and composition (environment: 6.5%; spatial: 6.3%; Table 4.12, Figure 4.17). Location, both spatial (broad and medium spatial scales) and environmental components of variation were significant in explaining patterns of composition. Both environmental effects and medium-scale spatial effects were significant in explaining patterns of α-diversity. Beta diversity was significantly explained by location (2.8%) and environmental (14.2%) effects and of the three taxonomic diversity measures had most of its variation explained (82.0%). For all three taxonomic diversity measures covarying effects explained large portions of variation in diversity patterns, especially in the shared variation explained by both environmental and spatial effects (Table 4.12).

Functional diversity in Malagasy nonvolant mammal communities could not be explained with a variation portioning model for FDiv (Table 4.12, Figure 4.17). The functional richness (FRic) of Malagasy nonvolant mammal communities was only significantly explained by environmental effects (11.3%); non-significant spatial effects (7.3%) and a large component of shared environmental and spatial covariation (16.6%) also contributed to the overall variation. Spatial effects (14.3%), particularly at medium spatial scales (12.8%), significantly explained FDis and a non-significant component of 8.4% was due to environmental effects. Environmental (15.9%) and spatial (21.9%, 17.3% at medium spatial scales) effects significantly explained the variation in RaoQ.

RaoQ, at 52.9%, had the most variation explained of the functional diversity measures (Table 4.12, Figure 4.17).

Environmental, spatial and biogeographic effects (Table 4.12, Figure 4.17) poorly explained phylogenetic diversity measures. Variation in MPD was not partitioned due to no forward selected variables. PDm had 6.9% of its variation significantly explained by medium scale spatial effects, and 20.7% of the variation was due to covariations between environmental and spatial variables. NTI had no significant components of variation explained; however, a combination of location, spatial and environmental effects explained 36.8% of its variation. PDm had the most variation (72.6%) explained of all other phylogenetic diversity measures.

The taxonomic diversity of Australian nonvolant mammal communities was variably attributed to environmental and spatial effects, which were significant for composition and β-diversity (Table 4.12, Figure 4.17). Alpha diversity had no significant component of variation due to pure effect types, and instead was mostly explained by covariations between location, environmental and spatial variables. Location (1.5%), environmental effects (6.7%) and broad scale spatial effects (5.4%) significantly explained variation in composition. Environmental effects explained 9.3% of the variation in β-diversity, more than double the 3.7% due to broad scale spatial effects (Table 4.12, Figure 4.17). Beta diversity had more of its variation (76.5%) explained than the two other taxonomic measures of diversity.

The functional diversity of Australian nonvolant mammal communities was also variably due to environmental and spatial effects (Table 4.12, Figure 4.17). Environmental effects (5.0%) and nonsignificant spatial effects at broad spatial scales (4.6%) explained variation in FRic. The variation in FDiv was not partitioned due to a lack of significant forward selected variables. Spatial effects at medium spatial scales

(7.4%) explained the only significant component of variation in FDis. Spatial scale effects (10.9%) were also significant for RaoQ, particularly at medium spatial scales (6.3%). Spatial effects at broad spatial scales (Table 4.12, Figure 4.17) predominantly explained variation in phylogenetic measures of diversity for Australian mammal communities. Spatial effects significantly explained 9.5% of the variation in PDm, 24.8% of the variation in MPD, and 6.0% of the variation in NRI. Location (3.7%) and environmental effects (6.2%) explained additional components of variation in MPD. Environmental effects also significantly explained 6.9% of the variation in MNTD and 7.0% of the variation in NRI. Of the phylogenetic diversity measures, MPD had the most variation explained (49.5%; Table 4.12).

Model 2

Detrended measures of taxonomic diversity for Malagasy nonvolant mammal communities all had significant components of variation explained by environmental effects (α: 2.6%, composition: 2.4%, β: 17.3%; Table 4.13). Alpha diversity and composition were also significantly explained by spatial effects, with significant medium-scale structures (2.9%) in α-diversity, and both medium (5.5%) and broad-scale (2.1%) structures in composition. Environmental effects (2.5%) and spatial effects at broad spatial scales (2.8%) significantly explained FRic. Variation in FDis and RaoQ was not partitioned due to no forward selected variables. PDm was the only measure of phylogenetic diversity partitioned, with significant environmental (2.7%) and spatial (3.2%, broad scale) components of variation. Beta-diversity provided the best-fitting detrended model, with 17. 3% of the variation explained (Table 4.13).

In Australian nonvolant mammal communities, α-diversity, FRic, FDis, PDm, and MNTD were not modeled with variation partitioning (Table 4.13). Composition, once

detrended, had the majority of its variation explained by broad scale spatial effects (5.2%) and some variation explained by environmental effects (3.8%). Environmental effects (12.6%) and broad-scale spatial effects (14.4%) significantly explained variation in beta diversity once detrended. Spatial effects at broad (11.4%) and medium (5.3%) spatial scales significantly explained RaoQ. Only environmental effects (24.4%) explained variation in MPD, and only spatial effects (22.4%) at broad spatial scales explained variation in NRI. Overall, detrended variation partition models explained less total variation in diversity for Madagascar and Australia than nondetrended diversity models.

Arboreal Mammal Communities: Variation Partitioning

Model 1

Malagasy arboreal mammal community α-diversity was significantly explained only by medium-scale spatial effects (9.0%), with a large component of variation also due to environmental-spatial covariation (7.3%; Table 4.12, Figure 4.18). In contrast, both environmental (6.1%) and spatial (8.8%) effects at broad (5.7%) and medium (3.8%) spatial scales significantly explained composition. Beta diversity, however, was significantly explained only by environmental effects (9.8%) with more of its variation due to covariation with other variables. Environmental effects explained a significant component of variation in FRic (11.7%). Spatial effects explained a nonsignificant component of variation in FDiv (7.1%) at broad spatial scales that was comparable to the significant component attributed to environmental effects (7.2%). FDis had no significant components of variation explained, with more variation attributed to the covariation between location, spatial and environmental variables. Spatial effects (13.6%) predominantly at medium spatial scales (9.3%) significantly explained variation in RaoQ

(Table 4.12, Figure 4.18). The majority of variation in phylogenetic diversity measures (PDm and MNTD) for Malagasy arboreal communities was due to spatial effects. For PDm, spatial effects significantly accounted for 31.8% of the variation, with 7.5% due to broad scale spatial effects and 28.2% of the variation due to medium scale spatial effects. Of all the diversity measures explaining patterns of Malagasy arboreal communities, β-diversity had the most variation explained by the variables tested in this study (88.6%).

The variation in Australian arboreal mammal community diversity was partitioned for composition, β-diversity, FDiv, RaoQ, PDm, NRI, and NTI (Table 4.12). No significant components of variation existed for composition or β, and the covariation between spatial effects and location explained a larger proportion of variation (10.1% and 13.9%, respectively) than any pure effect type (Table 4.12). The majority of variation explained in taxonomic measures of Australian arboreal mammal diversity was due to covariations between effect types. Functional divergence (FDiv) of Australian arboreal mammal communities was significantly explained by a combination of environmental (4.3%) and spatial (8.2%) effects at broad spatial scales. Only environmental effects (29.5%) significant explained variation in RaoQ. Only biogeographic effects explained variation in PDm (20.9%) and NTI (21.8%) for Australian arboreal mammal communities. Variation in MPD and NRI was predominantly due to covariations of effect types, and no pure component of variation was significant (Table 4.12, Figure 4.18).

Model 2

Detrended measures of arboreal mammal diversity in Madagascar included α, composition, β, FRic, FDiv, FDis, RaoQ, and MNTD (Table 4.13). Alpha diversity, FRic, FDiv, FDis, RaoQ and MNTD had no significant forward selected variables and did not have their variation partitioned. Composition and β-diversity had contrasting patterns of

assembly with composition significantly shaped by environmental (2.3%) and spatial (12.6%) effects at both broad (8.6%) and medium (4.3%) spatial scales. Only environmental effects (41.7%) significantly shaped beta diversity. Of the detrended measures of arboreal mammal diversity in Australia (composition, β, FDiv, MPD, and NRI) only FDiv had significant forward selected variables and underwent variation partitioning (Table 4.13). Biogeographic effects significantly explained 19.7% of the variation in in FDiv. Similar to nonvolant mammal communities, detrended variation partition models explained less total variation in diversity for Madagascar and Australia than nondetrended diversity models.

DISCUSSION

Patterns of nonvolant mammal diversity and community assembly in Madagascar and Australia had few convergent patterns of diversity and assembly, contrary to expectations. Despite similar biogeographic histories, patterns of insular mammal evolution, shared ecoregions, and convergent dietary niches in Australian possums and Malagasy lemurs, the taxonomic, functional and phylogenetic diversity of both nonvolant and arboreal mammal communities differed. Significant differences in diversity existed between Madagascar and Australia; however the assembly of nonvolant mammal communities was similar for taxonomic and functional diversity measures. Contrary to expectations, the differences in assembly patterns were greater for arboreal mammals than for all nonvolant mammals between Madagascar and Australia. In addition, shared ecoregions were significantly different from each other in climatic features potentially contributing to nonconvergent assembly processes in Madagascar and Australia.

Mammal Diversity Patterns

Nonvolant mammal and arboreal mammal diversity patterns were inter- and intra-regionally variable. I found some support for convergent patterns of niche evolution and community structure (cf. Smith and Ganzhorn 1996) for the mammals of Madagascar and Australia. Convergence in functional diversity values in the shared ecoregions of Madagascar and Australia (DES and TSMBF) existed for the functional divergence of nonvolant mammals in the DES ecoregion and the functional richness of nonvolant mammals in the TSMBF ecoregion. Functional richness values were also convergent for the arboreal mammal communities of the TSMBF ecoregion. The nonvolant mammals of the DES ecoregion in Madagascar and Australia also had similar taxonomic diversity, and phylogenetic diversity. Furthermore, across nonshared ecoregions patterns of diversity varied.

The presence of significant differences in diversity metrics describing nonvolant mammal and arboreal mammal communities is not wholly surprising when considering the faunal differences between Madagascar and Australia. Almost three quarters (71.8%) of Australia's nonvolant mammal species are terrestrial compared with 40.5% in Madagascar. Australia's terrestrial mammals have a higher average body size ($\bar{x}$ = 4589.4 g) than those in Madagascar ($\bar{x}$ = 312.4 g) and there are more non-folivorous herbivores (n = 23) in Australia than in Madagascar (n = 2). Australian mammals also comprise different locomotion types (gliding arboreal quadrupeds and species using hind-limb locomotion) than those in Madagascar (Table A.6 and A.9).

Functional convergence in dietary guilds has been demonstrated for the gliders and possums of Australia and lemurs of Madagascar (Smith and Ganzhorn 1996), which describes the majority of species in arboreal communities (Australia: 56%, Madagascar: 88%). In this study I used additional resource-related traits (body mass, trophic level,

habitat specificity, and torpor) and mammal species to Smith and Ganzhorn's (1996) test of convergence in diet, substrate use, and activity period between arboreal mammals in Madagascar and Australia. Madagascar's speciose arboreal communities comprised 88 species including strictly arboreal (78 species) and arboreal and terrestrial (10 species) species. By comparison, 28 species made up Australia's arboreal communities, with 21 strictly arboreal species and 7 species that were both arboreal and terrestrial. Within the arboreal species high dietary convergence on folivory was present, constituting 45% of the arboreal species in Madagascar and 47.6% of the arboreal species in Australia, in addition to convergence on gumnivory, insectivory and omnivory. Locomotion was distributed across three locomotion styles in both regions, with 53.8% of species in Madagascar and 71.4% of species in Australia using arboreal quadrupedalism. In addition, each region had its own unique locomotion category in vertical clinging and leaping present in the Indriids and *Lepilemur* genus of Madagascar and gliding arboreal quadrupedalism in the *Petauroides*, *Petaurus* and *Acrobates* genera of Australia. Madagascar's and Australia's arboreal communities were very different however in activity period. Madagascar's arboreal communities were comprised of mostly nocturnal species (n=54) and cathemeral and diurnal species occurred in equal amounts (12 species each). Australia had no diurnal arboreal species. Arboreal species also showed high ecoregion specificity in both regions, with more than 50% of each species pool composed of species confined to one ecoregion type. Finally torpor was present in a higher proportions in Australian arboreal species (6 species; 37.5% of data available) in comparison to Madagascar, were 18% of the species use torpor (n=11). Consequently, despite convergence in dietary guilds, and the presence of arboreal folivores in both regions, the activity periods, substrate preference and presence of torpor differentiate the two regions at the community level. This study found nonconvergent patterns in diversity

in the TSMBF ecoregion, and indicated the potential for convergence in singular traits in some arboreal taxa, but not at the community level.

Furthermore, contrary to previous studies (Olson and Dinnerstein 2002; Olson et al. 2001), shared ecoregions within Madagascar and Australia were not climatically similar (cf. Jepson and Whittaker 2002; Londoño-Murcia et al. 2010). Significant differences in seasonality values were found between the DES ecoregions of Madagascar and Australia, where higher precipitation seasonality was observed in Madagascar and higher temperature seasonality was observed in Australia (Table 4.10). In the TSMBF ecoregion annual mean temperature and temperature seasonality was lower in Madagascar, and elevation was lower in Australia. The significant seasonality differences detected in the DES ecoregion likely contribute to the significant differences in functional diversity between the two regions, despite convergent patterns of taxonomic and phylogenetic diversity. While the nonsignificant differences in DES might be due to the small sample size of DES study sites in Australia (n = 3), the presence of significant taxonomic and phylogenetic differences suggests that this result is not simply a sampling bias.

Phylogenetic diversity of nonvolant mammal communities was randomly structured in Madagascar and Australia with a tendency toward overdispersion. However, a few sites exhibited phylogenetic clustering in Australia. Furthermore, Australian nonvolant mammal communities had a wider range of phylogenetic diversity values for all measures than existed in Madagascar, perhaps reflecting the difference in colonization history and the presence of more mammal orders in Australia (5 represented in this study) in comparison to Madagascar's four. Arboreal communities in both regions were characterized by similar phylogenetic diversity values (except again for a large range in Australian communities) characterized by random phylogenetic structure. Although, in

Australia some communities were composed of species that co-occur more than expected by chance. These results are congruent with previous analyses that found general trends toward phylogenetic random or overdispersed phylogenetic structures in mammal communities (Cardillo et al. 2008, 2011; Cooper et al. 2008), and lineages with histories of rapid adaptive radiation, particularly in isolation (Cardillo 2011). Measures of phylogenetic diversity were not indicative of functional diversity, because all four community categorizations (nonvolant and arboreal mammal communities in Madagascar and Australia) had measures that were weakly correlated (consistent with the results of chapter 3).

Community Assembly

Nonvolant Mammal Communities

Overall, my results showed mixed support for convergent patterns of community assembly describing nonvolant mammal communities in Madagascar and Australia (Figure 4.17). The hypothesis that environmental effects and spatial effects, depicting environmental sorting and dispersal limitation by distance, explain taxonomic diversity of nonvolant mammal communities in Madagascar and Australia was somewhat supported. Community composition of nonvolant mammals was predominantly explained by a combination of spatial and environmental effects with similar total proportions of variation explained in both Madagascar (spatial: 6.3%; environmental: 6.5%) and Australia (spatial: 5.4%; environmental: 6.7%). In addition, spatial-environmental covariation explained large components of variation in diversity regardless of the taxonomic diversity measure used. There was mixed support for the hypothesis that functional diversity was shaped by deterministic processes. Instead in both Madagascar and Australia, environmental and spatial variables interacted to shape patterns of

mammal functional diversity, as was shown for Malagasy primate communities in chapter 3. Environmental effects, indicating environmental sorting, explained larger proportions of variation in functional richness patterns in Madagascar (11.3%) and Australia (5.0%), supporting the hypothesis that functional diversity is shaped by environmental sorting. However, a large but nonsignificant component of variation due to spatial broad scale spatial effects also existed. Covariation between location, environmental and spatial variables also explained large proportions of variation. Functional dispersion measures (FDis and RaoQ) in both Madagascar and Australia had large components of variation due to medium scale spatial effects, suggesting that dispersal limitation better explains trait distributions in Malagasy and Australian nonvolant mammal communities. However covariations with location and environmental effects also existed. RaoQ was also significantly explained by environmental effects in Madagascar. My results suggest that environmental sorting and dispersal limitation interact to shape patterns of taxonomic and functional diversity in Malagasy and Australian nonvolant mammal communities, but the proportion of variation explained varied by region.

Contrary to expectations, environmental sorting did not consistently explain the assembly of phylogenetic diversity in the nonvolant mammal communities of Madagascar and Australia. Furthermore, assembly patterns were regionally dependent. Environmental sorting in both Madagascar and Australia explained NTI; however, overall nonvolant mammal phylogenetic diversity was differentially shaped by assembly processes in both regions. Madagascar's phylogenetic diversity patterns were predominantly explained by spatial-environmental covariations (PDm, MNTD, and NRI). However, nonvolant mammal community phylogenetic diversity in Australia was more commonly explained by spatial effects or dispersal limitation (at broad spatial scales),

which were significant for PDm, MPD, and NRI. Madagascar's nonvolant mammal community assembly was shaped by pure environmental effects (NRI), medium-scale spatial effects (PDm), and covariation between environmental and spatial variables (PDm, MNTD, and NTI). The phylogenetic age of communities (PDm) was dependent upon medium-scale spatial effects and covariations between variables. The mean phylogenetic distances among taxa (NRI) indicated that nonvolant mammal communities were overdispersed. NRI had more variation explained by environmental sorting indicating phylogenetic convergence in traits that allow for environmental adaptations among non-related species (Cavender-Bares et al. 2004; Kembel 2009; Webb et al. 2002; Table 3.2). However the phylogenetic overdispersion indicated by NTI, MNTD was better explained, albeit weakly, by covariations between longitude, environmental variables and spatial variables. In contrast, Australian nonvolant mammal community phylogenetic diversity had better fitting models with the variables tested in this study, which were able to explain 17-49.5% of the variation in measures. Phylogenetic assembly patterns supported the combined role of environmental sorting and dispersal limitation in MPD and NRI. Almost 25% of the variation in the mean pairwise distance among species in a community (MPD) in Australia was explained by broad scale spatial effects. Dispersal limitation has likely led to the isolation of some communities with varied MPD values and resulted in spatial variables explaining the wide range of MPD values found in Australia, which were ecoregionally variable (Figure 8.4). The net relatedness index (NRI) provided evidence for overdispersion in the DES and TSMBF ecoregions but increasing presence of clustering in the rest of Australia. The phylogenetic age of nonvolant mammal communities (PDm) was only significantly explained by spatial effects at broad spatial scales.

Arboreal Mammal Communities

Patterns of arboreal mammal community assembly were not convergent across Madagascar and Australia (Figure 4.18). While taxonomic diversity of nonvolant mammal communities was best explained by a combination of environmental and spatial effects in Madagascar and Australia, spatial effects (except for β) significantly explained Malagasy arboreal communities. Instead, covarying effects between location, environmental effects, and spatial effects explained the majority of variation in taxonomic diversity of Australian arboreal mammal communities. In chapter 2, the composition of arboreal mammal communities and primate communities in Madagascar were found to be predominantly shaped by spatial effects, due to dispersal limitation compounded by an impassable matrix between sites (chapter 2), but Australian arboreal mammal communities were not strongly explained by either environmental or spatial effects. In Australia, the covariation between environmental variables and distance between sites shaped the taxonomic diversity of arboreal communities. Furthermore, the lack of significant medium scale spatial variables in both Madagascar and Australia indicate taxonomic diversity is ecoregionally structured, with occurrence of arboreal mammals occurring within specific bioclimatic zones.

Contrary to expectations, the assembly processes explaining functional diversity patterns in the arboreal mammal communities of Madagascar and Australia, were not similar. In Madagascar, environmental sorting predominantly explained functional richness and functional divergence. However, functional dispersion (FRic and RaoQ) was better explained by dispersal limitation by distance. In Australia, only two measures could be modeled. An impressive 86.8% of the variation in functional divergence was explained by a combination of environmental sorting, dispersal limitation and biogeographic dispersal barriers, of which dispersal limitation accounted for the largest

amount of variation. By contrast, RaoQ was only shaped by annual precipitation explaining 29% of the variation. Mixed support for the hypothesis that functional diversity is explained by environmental sorting and dispersal limitation existed, and patterns of assembly in arboreal mammals appear to be metric-specific. Furthermore, phylogenetic diversity of arboreal mammal communities in Madagascar and Australia did not have more of their variation explained by environmental sorting, contrary to expectations. In Madagascar phylogenetic diversity was weakly explained by the variables tested in this study. The phylogenetic age of arboreal communities in Madagascar (PDm) was significantly explained by broad and medium scale spatial variables accounting for 31.8% of the variation. The mean nearest taxon distance (MNTD) was explained by covariations between location, environmental and spatial variables. In contrast, Australian nonvolant mammal community phylogenetic diversity measured as PDm and NTI were only significantly explained by biogeographic dispersal barriers, specifically the isolation of sites due to water. However, for MPD and NRI, covariations between environment location and spatial effects explained the majority of phylogenetic variation in arboreal communities.

Australian arboreal mammal community phylogenetic diversity was the only group of diversity measures in this analysis to be significantly explained by biogeographic distance ratios, in this case traveling around permanent bodies of water. As previously mentioned, sampling particularly for arboreal species was biased to the eastern coastal regions from the north to the south. Eastern Australia's environments are strongly influenced by the Great Dividing Range, Australia’s largest mountain range along the east coast, and the Murray-Darling Basin, which maintains Australia’s largest and longest river complex (Byrne et al. 2008; Martin 2006). The Murray-Darling basin is in the southeast of Australia and is characterized by a heavy concentration of permanent river

systems (Figure 4.5). Rivers (including basins and valleys) result in genotypic differentiation in Australia for a variety of vertebrate species (e.g., Brown et al. 2006; Gongora et al. 2012; Hoskin et al. 2005; Lee et al. 2010; cf. Lee et al. 2013; Moritz et al. 2005; Moussalli et al. 2009; Potter et al. 2012) including two arboreal mammal species (*Petauraus* species, Firestone et al. 2002; *Phascolarctos cinereus*, Lee et al. 2010; cf. Lee et al. 2013). Significant biogeographic effects were not detected for the functional diversity of arboreal mammal communities in Australia. Thus, the difference in distribution of arboreal species is not likely to be caused by functional dispersal but the result of the isolation of particular clades that has produced biogeographically structured phylogenetic diversity patterns.

Overall, both nonvolant mammal and arboreal mammal communities were characterized by phylogenetically randomly structured communities, with tendencies towards phylogenetic overdispersion. Patterns of phylogenetic overdispersion are thought to be due to competition among phylogenetic and ecological relatives resulting in competitive exclusion or limiting similarity (Webb et al. 2002). However, similar traits can also evolve convergently in distantly related taxa and result in overdispersion through environmental sorting (Cavender-Bares et al. 2004; Kraft et al. 2007). Consequently, similar phylogenetic diversity values can imply various community assembly processes (Kraft et al. 2007; Pavoine and Bonsall 2011; Webb et al. 2002; Weiher et al. 2011). In this study, phylogenetic diversity and functional diversity were not strongly interrelated, and traits were chosen to reflect axes of resource-use. Functional diversity patterns in functional richness and functional divergence in Madagascar were significantly explained by environmental sorting, but dispersal limitation by distance explained more variation in functional dispersion (FDis and RaoQ). In Australia however, functional diversity measures were poorly explained and only two measures could be fit to a model.

Functional divergence was explained by a combination of environmental, spatial and biogeographic effects with broad scale spatial effects explaining the most variation. In contrast RaoQ was only explained by environmental effects, which accounted for 29.5% of its variation. The broad sampling scale and absence of significant environmental effects depicting environmental sorting in most phylogenetic diversity measures may indicate that competition at the local scale is contributing to observed phylogenetic diversity patterns in mammal communities (e.g., Cardillo 2008, 2011; Cooper et al. 2008; Kamilar and Guidi 2010; Kamilar et al. 2014) or that the random to overdispersed phylogenetic diversity measures detected cannot be explained by variables describing extant environments. In a study of Neotropical primate assemblages (Gavilanez and Stevens 2013), heterogeneous phylogenetic structures (MPD, MNTD, PDm) shaped by spatial effects, including dispersal limitation, with covarying environmental and historic effects were found. Both Madagascar's and Australia's mammal communities were shaped to some extent by spatial effects, with additional roles for environmental and biogeographic effects. Consequently, a combination of dispersal limitation, environmental sorting, and evolutionary history has shaped observed patterns of phylogenetic diversity in the mammals of Madagascar and Australia.

A Difference in Histories between Madagascar and Australia

Both Madagascar and Australia have histories of long periods of isolated faunal evolution, but their histories are not identical in form. Madagascar's mammal communities are the result of four independent colonizations during the Paleogene Period (Weyeneth et al. 2011) by over-water dispersal from mainland Africa (Ali and Huber 2010). Consequently, Madagascar's nonvolant mammal communities are the result of discrete colonization events and 23 million years of evolution in isolation. In contrast,

Australia has a much older and longer history of mammalian evolution starting with the monotremes 100 Ma (Archer et al. 1999), the marsupials 64–65 Ma (Woodburne and Case 1996), and rats 10–15 Ma and 2 Ma (Kay and Hoekstra 2008), continuing into the present with human introductions of other placental mammal species (e.g., *Canis lupus dingo*, *Felis catus, Vulpes vulpes*, etc.; Johnson 2006). The timing of the colonization events in Madagascar and Australia has left particular clades in isolation for longer than others. For example the marsupials of Australia were left to diversify in the absence of mammalian competitors (except for monotremes) until the arrival of rodents 5-10ma (Woodburne and Case 1996). By contrast Madagascar has had more frequent colonization events of potential competitors punctuating the evolution of its endemic mammalian fauna. First primates arrive 50-60 ma, followed by afrosoricidans 25-42 ma, rodents 20-24 ma and most recently carnivores 19-26 ma (Ali and Huber 2010). Consequently differences in phylogenetic diversity are to be expected, even in shared ecoregions.

The evolutionary history of mammal colonizations in Madagascar and Australia suggests a potential role for priority effects, a stochastic assembly process. Priority effects exist where early colonizing species affect the establishment and abundance of later colonizers (Ejrnæs et al. 2006; Leibold et al. 2004). While phylogenetic relatedness (or phylogenetic diversity) may be used as a surrogate for niche similarity (cf. Losos 2008; Losos et al. 2003; Swenson 2011; chapter 3) to model the contribution of competition and priority effects to community diversity (cf. Tan et al. 2012), phylogenetic diversity metrics (including PDm) are not highly sensitive to either mass or priority effects, even when trait variation is strongly conserved (Mason and Pavoine 2013). In contrast, functional diversity metrics (FRic, FDis, Rao) are better predictors of the contribution of priority effects to community assembly of species (Mason et al. 2013).

Communities in similar environments have differing species composition when formed by priority effects (Ejrnæs et al. 2006; Fukami et al. 2005), resulting in a disrupted relationship between traits and species occurrence (Mason et al. 2013). Both nonvolant mammals communities and arboreal mammal communities in Madagascar and Australia had overall weak correlations between functional and taxonomic measures of diversity. This mismatch between species' traits and species occurrence may indicate that priority effects are shaping observed patterns of diversity with early colonizers having a competitive advantage. Alternatively, the weak correlation between functional and phylogenetic diversity measures might also indicate the presence of labile traits or a mixture of conserved and labile traits (Losos 2008). In Madagascar's primate communities the weak correlation between functional and phylogenetic diversity is thought to be due to rapid diversification into novel niches early in lemur evolution resulting in patterns of phylogenetic overdispersion and trait convergence (chapter 3). Adaptive radiations into novel niches have also been suggested for the nonprimate mammal fauna of Madagascar (Muldoon and Goodman 2010) and Australia (e.g., Musser 2005; Rowe et al. 2008), which may also better explain patterns of extant functional and phylogenetic diversity than the contribution of priority effects.

Phylogenetic diversity differences between Madagascar and Australia may also be due to differences in diversification rates due to biological traits that increase speciation rate or lower extinction rate in a clade (Cardillo et al. 2003). Traits associated with life history patterns, sexual selection, body size and resource use have all been suggested to influence diversification rates (reviewed in Cardillo et al. 2003). Primate species with mutualistic associations with plant species had higher speciation rates, lower extinction rates and thereby higher diversification rates than non-mutualistic ones. Mutualistic extinct and extant primates had significantly larger geographic ranges which promoted

diversification (Gómez and Verdú 2012). Furthermore, body size, in a comparative analysis of all primates, was less important to diversification rates than clade-specific differences (FitzJohn 2010). Body size also had no association with diversification rate in Australian nonvolant mammals; however a relationship between geographic range size and litter size was found (Cardillo et al. 2003). Australia's terrestrial mammal species are much larger than the species occurring in Madagascar and Australia is a larger land mass favouring larger ranges in species distributions. The combination of older lineage age in Australia, higher cladistic diversity (with more orders present) and the potential differences in diversification rates due to life history and range size differences between Madagascar's and Australia's mammal species are all likely responsible for the significant differences present in phylogenetic diversity measures between the two regions in their nonvolant mammal communities. However, the absence of significant differences at the arboreal mammal level implies similar diversification rates and/or patterns of diversification resulting in similar phylogenetic diversity patterns in arboreal mammal communities.

Anthropogenic disturbance in the form of human land modification and the introduction of nonindigenous species can also influence observed patterns of extant mammal diversity and assembly. Humans arrived in Australia 50 ka (Bowler et al. 2003; Roberts et al. 1994; Turney et al. 2001) and arrived in Madagascar only 2.3 ka (Burney et al. 2004). With the arrival of humans both regions experienced large-scale extinctions of mammal species. In Madagascar, 29 mammals, including 17 primate species, a pygmy hippopotamus, *Plesiorycteropus madagascariensis*, and a giant fossa (Simons 1995) have gone extinct, which has potentially disrupted expected patterns of mammal diversity distributions and assembly (cf. Razafindratsima et al. 2013), although the extinction of

these species is unlikely to have led to patterns of extant patterns of phylogenetic overdispersion or functional diversity (*sensu* chapter 3).

Australia, however, has experienced two extinction events. The first was a megafaunal extinction event 46 ka (Miller et al. 2005; Roberts et al. 2001) when most mammal species > 10 kg went extinct (Flannery 1990a). This extinction event may have served as an extinction filter, removing extinction-prone large bodied mammals from Australia's species pool (Cardillo and Brohman 2001; Johnson 2002), differentiating the size distribution of extant mammals in Madagascar and Australia. More smaller-bodied mammals exist in Madagascar than in Australia, due in part to the timing and size-bias of their respective large-scale mammal extinctions. The second extinction event, more recent than Madagascar's, closely followed European settlement and the introduction of nonindigenous mammal species (Fisher et al. 2003). Eighteen species have gone extinct in Australia since 1600 (Baillie 1996; Maxwell et al. 1996). While nonindigenous species were excluded from assemblage lists, their competitive interactions with indigenous species cannot be ignored. In contrast to Madagascar, whose extinction losses are thought to be mainly due to fire disturbance and human hunting (Burney et al. 2004), the loss of Australian marsupials has most likely been a result of competition with nonindigenous species (e.g., *Vulpes vulpes* and *Felis catus*; Glen and Dickman 2008; Harris 2009; Johnson 2006), although resource depletion and habitat modification are also contributing factors (Woinarski et al. 2001). The loss of diversity in Madagascar due to subfossil mammal extinctions has potentially liberated previously occupied niches, which extant fauna have not yet evolved to exploit (Kamilar and Guidi 2010; Razafindratsima et al. 2013), whereas the nonindigenous species in Australia impose a continual negative presence on the diversity and detected assembly patterns of Australia's mammal communities.

Anthropogenic impacts on detected assembly patterns may be due to decreases in species distribution over time due to habitat modification. For example, in Australia the common brushtail possum (*Trichosurus vulpecula*) which was present throughout almost all of Australia in pre-European times, and the Hastings river mouse (*Pseudomys oralis*) which was present in less than two percent of Australia, now have ranges less than 40% of their pre-European sizes (Burbidge et al. 2008), or smaller (e.g., *Macrotis lagotis* and *Leporillus conditor*; Hanna and Cardillo 2013). Smaller home ranges that could result in range contractions have also been suggested in Malagasy mammal species, including *Propithecus diadema,* and *Hapalemur griseus* (reviewed in Irwin et al. 2010). The extant distributions of species in protected areas may be indicating relict populations and the assembly processes detected are likely compounded by ongoing habitat modification and anthropogenic change that exacerbates spatial patterning between sites with species dispersal constrained connected pieces of appropriate habitat (Lasky and Keitt 2013). Furthermore, climate change could result in disrupted environmental correlations due to a mismatch between species adaptation and habitat characteristics (c.f. Van der Putten et al. 2010).

Methodological Improvements and Future Directions

The spatial grain of the study was large (chapters 2 and 3), and the same sampling bias exists in Australia, which has implications for the detection of fine-scale assembly processes such as intra- and interspecific interactions that occur at local spatial scales (e.g., Kraft et al. 2007). Furthermore, the WWF ecoregion classification system is a broad spatial scale schema, created for conservation reasons, to allow comparisons between nations (Olson and Dinnerstein 2002). However, each ecoregion type is described by various levels of global diversity in subtype. For example, the TSMBF habitat type

includes 50 country-level ecoregions or 35% of all the terrestrial ecoregions globally. Consequently, this habitat classification describes a diverse array of biological richness and forest complexity that may be regionally dependent, which is consistent with the statistically significant differences found in this study between the climatic descriptions of shared ecoregions in Madagascar and Australia (Table 4.6). The WWF ecoregion classification system has been employed in a variety of studies (e.g., Cardillo 2011; Fritz et al. 2009; He and Zhang 2009; Thompson et al. 2005) and is suggested to be useful for broad-scale comparisons, setting conservation priorities, and minimizing species distribution errors. However, it has also been critiqued for overgeneralizing patterns of diversity and masking patterns of environmental heterogeneity (cf. Jepson and Whittaker 2002; Londoño-Murcia et al. 2010). Consequently, it may be inappropriate for comparing regions with varying levels of environmental heterogeneity for the study of community assembly. However, patterns of vertebrate diversity (amphibians, reptiles, birds, and mammals) suggest that species' natural spatial boundaries, such as are depicted by the WWF ecoregion system, shape correlation patterns between beta diversity and productivity differences globally (He and Zhang 2009). Furthermore, ecoregion classification in Madagascar, although at a finer scale than is used in the WWF classification schema (chapter 3), also strongly shapes patterns of diversity and assembly (at least for primates).

The size of ecoregions in Madagascar and Australia varied, resulting in smaller potential sample sizes per ecoregion (number of study sites) and potentially influencing the diversity patterns or assembly processes detected. Controlling for ecoregion size has been previously used in the study of the phylogenetic structure of carnivore assemblages in Africa, where no size effect was discovered (Cardillo 2011). However, future tests of convergence in diversity patterns across ecoregions might benefit from a size-explicit

approach due to diversity predictions associated with larger ecoregion sizes: (1) speciation is expected to increase with size (Kisel and Barraclough 2010; Losos and Schluter 2000), and (2) extinction rates in larger regions is expected to decrease (Purvis et al. 2005). Such size-dependent associations can result in varied patterns of phylogenetic diversity (cf. Cardillo 2011). The two shared ecoregions, TSMBF and DES, constitute very different surface areas in their respective countries. For example, compared to a small TSMBF ecoregion area in the northeast of Australia (44,490 km^2, n=9), the TSMBF ecoregion in Madagascar constitutes 60% of Madagascar's surface area (348,627 km^2) and contains twice the study sites (n=19) of the TSMBF ecoregion in Australia. In contrast the DES ecoregion is 57% of the surface area (4,421,006 km^2) of Australia, compared to 25% of the surface area (145,178 km^2) of Madagascar.

Furthermore, Madagascar is a smaller land mass than Australia, and is characterized by large agricultural regions between protected areas (DeFries et al. 2005; Harper et al. 2007). Australia by contrast, has urban centers situated between protected areas (cf. Ikin et al. 2014; Ramp et al. 2006). The nature of the matrix between sites and the proximity of heavily populated human settlements between protected areas also influences observed diversity patterns (cf. Lasky and Keitt 2013). Although variables associated with anthropogenic disturbance were not explicitly tested in this study, the inclusion of the size of the protected area and the age of the protected area did indicate that especially in Australia, protected area size and age is related to mammal community diversity. However, the correlations with age should be interpreted with some caution because the gazetting time periods for the sites in Australia were highly biased. Further research partitioning out the proportion of variation due to anthropogenic disturbance is needed to identify to what degree the detected patterns of environmental sorting and dispersal limitation is mediated by ongoing habitat modification.

Sampling effects between two regions composed of different species pools can create issues for comparison because pools of higher species richness (α) have a greater probability of higher functional diversity and phylogenetic diversity values because trait values and/or phylogenetic differences will accumulate with the number of species (Calba et al. 2014). Furthermore, by collating occurrence data from several sources variation in sampling intensity may also result in diversity differences. Madagascar and Australia had significant differences in α-diversity for both nonvolant and arboreal mammal communities, with Madagascar having higher values in both cases. However, functional richness measures and PDm (the phylogenetic combined age of communities) were both higher in Australia, negating this potential cause of arbitrary significant results between regions. Furthermore, species richness and area relationships (SARs) did not exist for nonvolant mammal communities in Madagascar or Australia or for arboreal mammal communities in Madagascar. However, a significant positive SAR did exist for Australian arboreal mammal communities. Consequently, a sampling effect that could result in higher trait and phylogenetic diversity with protected area size due to higher number of species may exist in Australia. However, only functional richness (FRic) and the phylogenetic diversity measure (PDm) had strong relationships with species richness in Australian arboreal mammal communities (Figure 4.15.D). Consequently, it is unlikely that area effects are driving the diversity relationships across measures. Species richness was also not related to protected area age for the nonvolant mammal communities of Madagascar or the arboreal mammal communities of Madagascar and Australia. However a significant negative relationship existed between Australian nonvolant mammal community species richness and protected area age, which was due to differentiation in the time periods association with park gazetting.

Conclusions

Patterns in nonvolant mammal diversity and community assembly in Madagascar and Australia were inter- and intra-regionally variable. Despite similar biogeographic histories, patterns of insular mammal evolution, shared ecoregions, and convergent niches in Australian possums and Malagasy lemurs, support for convergent diversity and assembly patterns only existed for nonvolant mammals. Arboreal mammals had convergent functional richness values but did not share patterns of assembly. Furthermore, the WWF ecoregional classification used to compare shared habitat types were actually environmentally significantly different. This analysis calls into question the search for overarching explanations for patterns of diversity or assembly when significant environmental heterogeneity and variations in diversity characterize mammal communities. Broad-scale regional descriptions of community assembly patterns may be unrealistic even for regions with comparable histories. Overall, patterns of mammal diversity in Madagascar and Australia were the combined result of environmental sorting, dispersal limitation, and evolutionary processes. This study provides further evidence that assembly processes do not operate in isolation but work in concert to shape patterns of community diversity.

Taxonomic mammal diversity in both Madagascar and Australia was shaped by the combined actions of variables depicting environmental sorting and dispersal limitation by distance. In addition, spatial-environmental covariation explained large components of variation in most diversity measures that could be modeled. Phylogenetic diversity across groups was variably explained by environmental sorting, dispersal limitation by distance and biogeographic barriers. Phylogenetic overdispersion characterized the phylogenetic diversity of both Malagasy and Australian mammal communities and the phylogenetic diversity differences between the two regions are

likely due to widespread isolated lineage diversification in each region. Furthermore though both Madagascar and Australia have experienced large megafaunal extinction events, their impacts are not readily apparent in extant diversity patterns. Instead ongoing anthropogenic modification, the impact of nonindigenous competitors and the ecogeographic variation that characterize the ecoregions of Madagascar and Australia have resulted in diverse mammal communities that are the result of both environmental sorting and dispersal limitation. Furthermore, the use of phylogenetic diversity as a proxy measure for functional diversity in Malagasy and Australian mammal communities is inappropriate and can lead to erroneous conclusions regarding their ecological and evolutionary histories.

Convergence in individual traits can result in superficial similarities between species in disparate regions. However, traits occur as part of a larger trait assemblage in a species due to ontogenetic differences or natural selection. Consequently, despite the high proportion of folivorous arboreal species in both Madagascar and Australia, convergent diversity patterns or assembly patterns at the community level were not found for arboreal communities. Interestingly however, they were found for nonvolant mammal communities in Madagascar and Australia. The diversity of ecoregions insulated evolutionary patterns and community-level averaging effects of a few unique traits, have resulted in nonvolant community structures with convergent patterns in the dry and xeric forest regions of Madagascar and Australia and broadly similar assembly patterns across ecoregions. Within and across diversity measures and biogeographic regions differences in process exist with mechanistic implications. The study of community assembly will consequently continue to benefit from a scale-explicit and regionally-explicit approach to the study of community assembly and a concerted effort to understand the proximate mechanisms driving observed patterns of mammal diversity.

Table 4.1. Shared and nonshared ecoregions between Madagascar and Australia according to the WWF classification of major habitat types (hereafter ecoregions; Olson et al. 2001). The ecoregion delineations are assigned based on similarities in climate, floristic structure, and patterns of diversity (Olson and Dinerstein 1998; Olson et al. 2001).

Shared Ecoregions	Nonshared Ecoregions
• deserts and xeric shrublands (DES) [1] • tropical and subtropical moist broadleaf forests (TSMBF) [2] • mangroves [3]	• tropical and subtropical dry broadleaf forests (TSDBF) • temperate broadleaf and mixed forests (TBMF) • temperate grasslands, savannahs, and shrublands (TGSS) • tropical and subtropical grasslands, savannahs, and shrublands (TSGSS) • Mediterranean forests, woodlands and scrub (MWFS) • montane grasslands and shrublands [3]

[1] Characterized by high rainfall and temperature variability, with evaporation generally exceeding rainfall (WWF 2014).
[2] Characterized by low temperature variability and high rainfall (> 200 cm annually). Forests are dominated by semi-evergreen and evergreen deciduous tree species (WWF 2014).
[3] no sites present in this ecoregion in this study.

Table 4.2. ANOVA results for significant differences in diversity (not detrended) between shared ecoregions in Australia and Madagascar. Bolded results are non-significant differences in diversity between Madagascar and Australia in shared ecoregions. No arboreal communities of five or more species existed in both Madagascar and Australia for DES and TSMBF, making a statistical comparison impossible. Bolded values are non-significant differences between Madagascar and Australia. DES: Deserts and Xeric Shrublands; TSMBF: Tropical and Subtropical Moist Broadleaf Forests.

	DES		**TSMBF**	
Diversity Measure	***F*-value**	***p*-value**	***F*-value**	***p*-value**
All Nonvolant Mammals				
Alpha	1.96	**0.192**	18.31	<0.000
Beta	2.73	**0.129**	18.65	<0.000
FRic	9.689	0.010	3.757	**0.064**
FDiv	3.17	**0.103**	4.69	0.040
FDis	13.07	0.004	21.05	<0.000
RaoQ	18.41	0.001	39.37	<0.000
PDm	0.10	**0.759**	5.084	0.033
MPD	130.10	<0.000	67.31	<0.000
MNTD	1.12	**0.315**	7.135	0.013
NRI	0.311	**0.589**	31.19	<0.000
NTI	4.741	**0.054**	34.83	<0.000
Arboreal Mammals				
Alpha			15.84	<0.000
Beta			73.87	<0.000
FRic			2.12	**0.159**
FDiv			11.30	0.003
FDis			9.06	0.022
RaoQ			10.51	0.004
PDm			5.275	0.031
MPD			12.85	0.001
MNTD			0.86	**0.362**
NRI			9.85	0.004
NTI			7.57	0.011

Abbreviations: FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index

Table 4.3. Linear regressions of diversity measures on species richness (α-diversity) in Madagascar and Australia. Log linear regressions are not reported as they showed similar trends. Adjusted R^2 values are shown with a "+" or "-" in parentheses to indicate the direction of the linear trend, if significant.

Diversity Measure	**Madagascar Species Richness**		**Australia Species Richness**	
	Adj.R^2	***p*-value**	**Adj.R^2**	***p*-value**
All Nonvolant Mammals				
Beta (1st PCoA Axis)	0.741 (-)	<0.000	0.613 (-)	<0.000
FRic	0.685 (+)	<0.000	0.912 (+)	<0.000
FDis	0.368 (-)	<0.000	-0.013	0.550
FDiv	-0.016	0.501	-0.017	0.694
RaoQ	0.468 (-)	<0.000	-0.020	0.990
PDm	0.920 (+)	<0.000	0.909 (+)	<0.000
MPD	0.078	0.060	0.015	0.187
MNTD	0.610 (-)	<0.000	0.433 (-)	<0.000
NRI	0.527 (-)	<0.000	0.116 (-)	0.008
NTI	0.191 (-)	0.006	<0	0.733
Arboreal Mammals				
Beta (1st PCoA Axis)	0.439 (-)	<0.000	<0	0.646
FRic	0.639 (+)	<0.000	0.818 (+)	<0.000
FDis	0.321 (-)	<0.000	0.138 (+)	0.024
FDiv	0.168 (-)	0.009	0.032	0.172
RaoQ	0.383 (-)	<0.000	0.101 (+)	0.048
PDm	0.564 (+)	<0.000	0.732 (+)	<0.000
MPD	0.182 (-)	0.007	<0	0.899
MNTD	0.596 (-)	<0.000	0.152 (-)	0.019
NRI	0.156 (+)	0.012	<0	0.866
NTI	0.002	0.194	<0	0.399

Abbreviations: FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index

Table 4.4. Alpha diversity relationships with the size of the protected area (Area) and the duration of protection (Age) for 34 nonvolant mammal communities in Madagascar, and 51 nonvolant mammal communities in Australia. Area and age data are available in Table A.3 and A.4.

	Madagascar			Australia		
	Area (km^2)		Age (years)	Area (km^2)		Age (years)
Model	**Summary statistics**	**AIC**	**Summary statistics**	**Summary statistics**	**AIC**	**Summary statistics**
Linear model	t = -0.721 p = 0.476 adj.R^2 = -0.015	256.316	t = -0.521 p = 0.606 adj.R^2 = -0.022	t = -0.627 p = 0.534 adj.R^2 = -0.012	383.014	t = **-2.497** p = **0.016** adj.R^2 = **0.095**
Arrhenius (Power) model [1]	t = 0.357 p = 0.724	256.706	nt	t = 0.088 p = 0.930	383.413	nt
Log-Arrhenius model	t = 0.627 p = 0.535 adj.R^2 = -0.019	42.919	nt	t = -0.311 p =0.757 adj.R^2 = -0.018	92.686	nt
Gleason (log-log linear) model	t = 0.412 p = 0.683 adj.R^2 = -0.026	256.685	nt	t = 0.089 p = 0.929 adj.R^2 = -0.020	383.413	nt

nt, not tested. Degrees of freedom for all models was 32 for Madagascar and 49 for Australia.
[1] summary statistics reported for the z value (the exponent) in the model; no adj.R^2 provided.

Table 4.5. Alpha diversity relationships with the size of the protected area (Area) and the duration of protection (Age) for 34 arboreal mammal communities in Madagascar, and 30 arboreal mammal communities in Australia. Area and age data are available in Table A.3 and A.4. Bolded values are significant.

	Madagascar			Australia		
	Area (km^2)		Age (years)	Area (km^2)		Age (years)
Model	**Summary statistics**	**AIC**	**Summary statistics**	**Summary statistics**	**AIC**	**Summary statistics**
Linear model	t = -0.346 p = 0.732 adj.R^2 = -0.027	188.793	t = -0.388 p = 0.701 adj.R^2 = -0.026	t = **2.138** p = **0.041** adj.R^2 = **0.110**	143.191	t = 0.182 p = 0.857 adj.R^2 = -0.034
Arrhenius (Power) model [1]	t = 0.780 p = 0.441	188.203	nt	t = **3.863** p < **0.001**	132.869	nt
Log-Arrhenius model	t = 1.100 p = 0.279 adj.R^2 = 0.006	14.242	nt	t = **4.361** p < **0.001** adj.R^2 = **0.383**	-0.109	nt
Gleason (log-log linear) model	t = 0.856 p = 0.399 adj.R^2 = -0.008	188.151	nt	t = **4.284** p < **0.001** adj.R^2 = **0.374**	132.605	nt

nt, not tested. Degrees of freedom for all models was 32.

[1] summary statistics reported for the z value (the exponent) in the model; no adj.R^2 provided.

Table 4.6. Environmental variables used in this study compared across the two ecoregions (DES and TSMBF) shared by Madagascar and Australia. Bolded values are significant differences (t-test) between the country's ecoregional climatic variables. DES: Deserts and Xeric Shrublands; TSMBF: Tropical and Subtropical Moist Broadleaf Forests.

	DES						**TSMBF**					
	Madagascar (n = 10)		**Australia (n = 3)**		**T-test**		**Madagascar (n = 18)**		**Australia (n = 8)**		**T-test**	
Variable (unit)	**Range**	**Mean**	**Range**	**Mean**	***t***	***p***	**Range**	**Mean**	**Range**	**Mean**	***t***	***p***
Annual Mean Precipitation (mm)	441.2-924.8	694.3	255.2-425.0	332.1	-5.19	**0.002**	1102.0-2429.0	1583	1012.0-2879.0	1705	0.512	0.620
Precipitation Seasonality ([1])	55.0-129.7	99.0	56.4-78.7	68.92	-2.89	**0.019**	42.4-107.0	76.3	73.4-89.9	81.1	1.02	0.320
Annual Mean Temperature (ºC)	212.3-259.0	237.6	228.3-239.2	234.6	-0.511	0.621	158.1-223.4	193.7	193.9-227.9	212.5	3.19	**0.004**
Temperature Seasonality ([2])	2238.0-3029.0	2616	5346.0-5936.0	5691	15.77	**<0.001**	1621.0-2634.0	2285	2249.0-3611.0	2944	4.20	**0.002**
Elevation (m)	27.4-912.3	311.9	121.1-244.4	183.5	-1.091	0.300	384.4-1698.0	1052.0	431.9-1018.0	616.0	-4.04	**<0.001**

[1] Coefficient of variation
[2] Standard deviation *100

Table 4.7. Comparison of straight line (Euclidean) and biogeographic effective distances (including biogeographic barriers) between study sites in Madagascar and Australia. Site averages, calculated from a site-by-site distance matrix, are presented. The biogeographic effective distance ratio is the ratio of each biogeographic effective distance to the Euclidean distance. It is a measure of how isolated a site is, and considers the unique role different biogeographic barriers have on the effective dispersal distance between sites.

	Euclidean distance (km)	**Island edge**	**Permanent Water bodies**	**Elevation changes**
Madagascar (n=34) Nonvolant Mammal and Arboreal Community Sites				
		Biogeographic effective distances (km)		
Mean ± SD	562.8±94.9	598.5±102.0	596.5±101.3	608.2±104.8
Range	434.2-795.0	461.8-843.9	460.8-847.7	467.4-862.2
		Biogeographic effective distance ratios		
Mean ± SD		1.06±0.01	1.06±0.01	1.08±0.02
Range		1.05-1.12	1.03-1.11	1.06-1.13
Australia (n=51) Nonvolant Mammal Community Sites				
		Biogeographic effective distances (km)		
Mean ± SD	1056.4±253.8	1121.4±269.5	1703.5±381.4	n/a
Range	819.2-2209.6	870.4-2327.4	920.7-2733.7	n/a
		Biogeographic effective distance ratios		
Mean ± SD		1.06±0.02	1.89±0.92	n/a
Range		1.00-1.07	1.00-4.45	n/a
Australia (n=29) Arboreal Community Sites				
		Biogeographic effective distances (km)		
Mean ± SD	859.1±283.8	911.8±303.9	1582.54±446.4	n/a
Range	602.6-1461.8	641.6-1563.9	662.27-2301.4	n/a
		Biogeographic effective distance ratios		
Mean ± SD		1.05±0.02	2.44±1.50	n/a
Range		1.00-1.08	1.00-6.06	n/a

Table 4.8. Forward selection of variables and RDA results for non-linearly detrended nonvolant mammal diversity in Madagascar and Australia.

		ANOVA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj.R^2**	***F*-value**	***p*-value**
Madagascar							
Alpha	Location	12.715	<0.000	Longitude	0.416	24.565	0.001
	Environment	10.140	<0.000	TempSeas	0.478	31.239	<0.000
				AnnPrecip	0.592	9.966	0.003
	Biogeography	1.617	0.223	n/a			
	Protected Area	0605	0.565	n/a			
	Spatial (PCNMs)	6.276	0.002	PCNM2	0.187	8.579	0.006
				PCNM1	0.337	8.239	0.012
				PCNM5	0.425	5.770	0.023
				PCNM4	0.510	6.213	0.015
				PCNM8	0.573	5.223	0.027
				PCNM7	0.628	5.145	0.031
Comp.	Location	6.566	<0.000	Longitude	0.209	9.700	0.001
				Latitude	0.252	2.866	0.001
	Environment	4.186	<0.000	TempSeas	0.180	8.239	<0.000
				Elevation	0.266	4.767	<0.000
				AnnPrecip	0.309	2.928	<0.000
				AnnTemp	0.322	1.553	0.020
	Biogeography	1.673	0.015	Edge	0.051	2.764	0.004
	Protected Area	1.106	0.290	n/a			
	Spatial (PCNMs)	2.910	<0.000	PCNM2	0.121	5.550	0.001
				PCNM1	0.210	4.591	0.001
				PCNM5	0.261	3.155	0.002
				PCNM4	0.294	2.399	0.001
				PCNM6	0.321	2.143	0.004
				PCNM7	0.338	1.734	0.025
				PCNM3	0.353	1.615	0.042
Beta[1]	Location	23.861	<0.000	Longitude	0.478	31.222	0.001
				Latitude	0.581	8.845	0.002
	Environment	17.225	<0.000	TempSeas	0.411	23.998	<0.000
				Elevation	0.623	18.993	<0.000
				AnnPrecip	0.704	9.574	<0.000
	Biogeography	2.227	0.034	Edge	0.100	4.657	0.012
	Protected Area	1.114	0.331	n/a			
	Spatial (PCNMs)	7.982	<0.000	PCNM2	0.260	12.606	0.001
				PCNM1	0.453	12.282	0.001
				PCNM5	0.574	9.833	0.001
				PCNM4	0.636	6.118	0.005
				PCNM7	0.670	4.004	0.027
FDis	Location	4.952	0.017	Latitude	0.181	8.301	0.004
	Environment	2.713	0.041	PrecipSeas	0.155	7.044	0.014
				Elevation	0.260	5.579	0.024
	Biogeography	0.541	0.662	n/a			
	Protected Area	0.073	0.938	n/a			
	Spatial (PCNMs)	2.544	0.032	PCNM1	0.197	9.091	0.007
				PCNM8	0.274	4.394	0.039
				PCNM2	0.345	4.365	0.046

Table 4.8 (continued)

		ANOVA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj.R^2**	***F*-value**	***p*-value**
FDiv	Location	0.519	0.591	n/a			
	Environment	0.364	0.869	n/a			
	Biogeography	1.682	0.190	n/a			
	Protected Area	0.387	0.697	n/a			
	Spatial (PCNMs)	1.010	0.437	n/a			
FRic	Location	5.316	0.008	Longitude	0.157	7.127	0.011
	Environment	7.828	0.001	TempSeas	0.365	19.972	<0.000
				AnnPrecip	0.445	5.611	0.026
	Biogeography	3.083	0.082	n/a			
	Protected Area	1.127	0.322	n/a			
	Spatial (PCNMs)	4.561	0.009	PCNM4	0.191	8.796	0.011
				PCNM5	0.293	5.607	0.016
				PCNM2	0.386	5.718	0.027
RaoQ	Location	5.887	0.005	Longitude	0.224	10.508	0.003
	Environment	3.261	0.013	PrecipSeas	0.196	9.034	0.005
				Elevation	0.289	5.189	0.030
	Biogeography	0.438	0.726	n/a			
	Protected Area	0.051	0.949	n/a			
	Spatial (PCNMs)	3.101	0.008	PCNM1	0.241	11.474	0.005
				PCNM8	0.355	6.670	0.010
PDm	Location	13.452	<0.000	Longitude	0.430	28.858	0.001
	Environment	9.503	<0.000	TempSeas	0.371	20.485	<0.000
				AnnPrecip	0.530	11.825	0.002
	Biogeography	2.757	0.038	Edge	0.191	8.779	0.002
	Protected Area	1.108	0.329	n.√a			
	Spatial (PCNMs)	9.891	<0.000	PCNM2	0.260	12.590	0.005
				PCNM1	0.383	7.358	0.016
				PCNM8	0.502	8.460	0.010
				PCNM7	0.571	5.776	0.029
				PCNM5	0.631	5.722	0.021
				PCNM4	0.682	5.552	0.020
MPD	Location	0.218	0.125	n/a			
	Environment	1.016	0.414	n/a			
	Biogeography	2.084	0.121	n/a			
	Protected Area	0.611	0.545	n/a			
	Spatial (PCNMs)	1.067	0.419	n/a			
MNTD	Location	8.032	0.002	Longitude	0.311	15.904	0.002
	Environment	5.098	0.002	AnnPrecip	0.256	12.340	<0.000
				TempSeas	0.349	5.578	0.025
	Biogeography	1.402	0.275	n/a			
	Protected Area	0.108	0.905	n/a			
	Spatial (PCNMs)	2.677	0.029	PCNM2	0.171	7.809	0.013
				PCNM1	0.330	8.621	0.008
NRI	Location	8.870	0.003	Longitude	0.282	13.957	0.002
	Environment	4.059	0.008	AnnTemp	0.239	11.388	0.002
				TempSeas	0.323	4.961	0.033
	Biogeography	3.838	0.014	Edge	0.213	9.953	0.002
	Protected Area	1.000	0.383	n/a			
	Spatial (PCNMs)	2.901	0.021	PCNM1	0.118	5.435	0.027
				PCNM7	0.230	5.657	0.023

Table 4.8 (continued)

		ANOVA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj.R^2**	***F*-value**	***p*-value**
NTI	Location	2.830	0.076	n/a			
	Environment	2.605	0.046	TempSeas	0.149	6.794	0.015
				AnnPrecip	0.242	7.043	0.012
	Biogeography	1.375	0.261	n/a			
	Protected Area	4.562	0.019	NS			
	Spatial (PCNMs)	2.155	0.072	n/a			
Australia							
Alpha	Location	19.311	<0.000	Longitude	0.426	38.180	0.001
	Environment	6.097	<0.000	TempSeas	0.266	19.144	<0.000
				AnnPrecip	0.368	8.894	<0.000
	Biogeography	6.636	0.002	Water	0.187	12.512	0.001
	Protected Area	3.275	0.035	Age	0.095	6.236	0.018
	Spatial (PCNMs)	3.966	<0.000	PCNM1	0.323	24.854	0.001
				PCNM2	0.440	11.201	0.004
Comp.	Location	7.441	<0.000	Longitude	0.143	9.365	0.001
				Latitude	0.205	4.793	0.001
	Environment	4.572	<0.000	AnnPrecip	0.112	7.304	<0.000
				TempSeas	0.218	7.651	<0.000
				AnnTemp	0.243	2.596	<0.000
				PrecipSeas	0.256	1.797	0.007
				Elevation	0.263	1.454	0.491
	Biogeography	2.869	<0.000	Water	0.054	3.881	<0.000
				Edge	0.069	1.794	0.021
	Protected Area	3.191	<0.000	Age	0.068	4.672	<0.000
	Spatial (PCNMs)	2.696	<0.000	PCNM1	0.120	7.785	0.001
				PCNM2	0.200	5.927	0.001
				PCNM3	0.246	3.899	0.002
				PCNM6	0.267	2.358	0.001
				PCNM5	0.286	2.274	0.001
Beta[2]	Location	29.198	<0.000	Longitude	0.384	32.232	0.001
				Latitude	0.530	16.178	0.001
	Environment	16.656	<0.000	AnnPrecip	0.292	21.711	<0.000
				TempSeas	0.563	31.349	<0.000
				PrecipSeas	0.597	5.033	0.004
				Elevation	0.613	2.945	0.042
	Biogeography	7.082	<0.000	Water	0.151	9.867	<0.000
				Edge	0.196	3.744	0.016
	Protected Area	6.200	<0.0000	Age	0.172	11.371	<0.000
	Spatial (PCNMs)	8.428	<0.000	PCNM1	0.326	25.179	0.001
				PCNM2	0.509	19.253	0.001
				PCNM3	0.603	12.450	0.001
				PCNM6	0.636	5.280	0.003
				PCNM5	0.657	3.762	0.019

Table 4.8 (continued)

		ANOVA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj.R^2**	***F*-value**	***p*-value**
FDis	Location	8.95	0.001	Latitude	0.192	12.910	0.002
				Longitude	0.241	4.158	0.049
	Environment	4.959	<0.000	Elevation	0.197	13.242	<0.000
				PrecipSeas	0.247	4.250	0.042
				TempSeas	0.310	5.427	0.0244
	Biogeography	0.067	0.926	n/a			
	Protected Area	1.909	0.141	n/a			
	Spatial (PCNMs)	3.180	0.010	PCNM2	0.227	15.696	0.003
				PCNM8	0.282	4.741	0.033
				PCNM1	0.327	4.211	0.043
FDiv	Location	4.492	0.019	NS			
	Environment	1.351	0.249	n/a			
	Biogeography	0.301	0.736	n/a			
	Protected Area	4.841	0.015	Age	0.101	6.620	0.014
	Spatial (PCNMs)	1.543	0.130	n/a			
FRic	Location	20.467	<0.000	Longitude	0.428	38.455	0.001
	Environment	9.877	<0.000	TempSeas	0.337	26.375	<0.000
				AnnPrecip	0.470	13.386	<0.000
	Biogeography	6.888	0.003	Water	0.194	13.098	0.001
	Protected Area	5.206	0.008	Age	0.145	9.515	0.003
	Spatial (PCNMs)	4.657	<0.000	PCNM1	0.367	29.946	0.001
				PCNM2	0.445	7.928	0.013
				PCNM6	0.489	5.104	0.028
RaoQ	Location	9.697	<0.000	Latitude	0.176	11.665	0.003
				Longitude	0.258	6.435	0.020
	Environment	5.358	0.002	Elevation	0.216	14.761	<0.000
				PrecipSeas	0267	4.446	0.041
				TempSeas	0.315	4.330	0.045
	Biogeography	0.285	0.766	n/a			
	Protected Area	1.488	0.239	n/a			
	Spatial (PCNMs)	4.067	<0.000	PCNM2	0.306	23.050	0.001
				PCNM7	0.560	5.130	0.023
				PCNM8	0.411	5.186	0.026
PDm	Location	4.439	0.021	Longitude	0.168	7.652	0.01
	Environment	4.582	<0.000	TempSeas	0.256	18.220	<0.000
	Biogeography	5.274	0.006	Water	0.137	8.925	0.004
	Protected Area	2.525	0.071	n/a			
	Spatial (PCNMs)	3.634	0.006	PCNM2	0.168	7.686	0.007
				PCNM8	0.316	7.895	0.008
				PCNM7	0.313	4.035	0.050
MPD	Location	6.482	<0.000	Latitude	0.161	40.626	0.005
	Environment	3.949	0.008	TempSeas	0.260	18.580	<0.000
	Biogeography	1.213	0.312	n/a			
	Protected Area	9.214	<0.000	Age	0.220	15.147	<0.000
	Spatial (PCNMs)	4.148	0.001	PCNM1	0.255	18.158	0.001
				PCNM6	0.338	7.095	0.016
				PCNM5	0.386	4.788	0.027
				PCNM2	0.429	4.452	0.043

Table 4.8 (continued)

		ANOVA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj.R^2**	***F*-value**	***p*-value**
MNTD	Location	3.631	0.036	Longitude	0.101	6.641	0.018
	Environment	2.691	0.044	AnnPrecip	0.141	9.236	0.003
	Biogeography	2.248	0.141	n/a			
	Protected Area	2.888	0.082	n/a			
	Spatial (PCNMs)	1.784	0.079	n/a			
NRI	Location	13.314	0.001	Latitude	0.279	20.394	0.001
				Longitude	0.330	4.695	0.032
	Environment	7.277	0.001	TempSeas	0.414	36.279	<0.000
	Biogeography	2.767	0.071	n/a			
	Protected Area	17.319	<0.000	Age	0.369	30.308	<0.000
	Spatial (PCNMs)	5.198	<0.000	PCNM1	0.404	34.939	0.001
				PCNM4	0.441	4.182	0.032
NTI	Location	2.912	0.064	n/a			
	Environment	2.328	0.066	n/a			
	Biogeography	0.178	0.842	n/a			
	Protected Area	1.902	0.161	n/a			
	Spatial (PCNMs)	1.697	0.103	n/a			

[1] First 3 PCoA axes of the Jaccard index

[2] First 2 PCoA axes of the Jaccard index

Abbreviations: Comp., composition; FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index; AnnTemp, Annual mean temperature; TempSeas, Temperature seasonality; AnnPrecip, Annual mean precipitation; PrecipSeas, Precipitation seasonality; PCNM, Principal Coordinate of Neighbour Matrices; n/a, not applicable because not significant; NS, no variable selected

Table 4.9. Forward selection of variables and RDA results for linearly detrended nonvolant mammal diversity in Madagascar and Australia.

		ANOVA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj.R^2**	***F*-value**	***p*-value**
Madagascar							
Alpha	Environment	4.269	0.008	TempSeas	0.224	10.556	0.004
	Biogeography	0.009	0.998	n/a			
	Protected Area	0.944	0.389	n/a			
	Spatial (PCNMs)	2.004	0.084	n/a			
Comp.	Environment	1.466	0.003	PrecipSeas	0.051	2.777	<0.000
	Biogeography	0.980	0.509	n/a			
	Protected Area	0.910	0.650	n/a			
	Spatial (PCNMs)	1.342	0.002	PCNM4	0.039	2.346	0.003
				PCNM6	0.061	1.746	0.016
				PCNM2	0.083	1.757	0.022
Beta[1]	Environment	3.308	0.002	PrecipSeas	0.173	7.897	<0.000
	Biogeography	0.876	0.523	n/a			
	Protected Area	0.564	0.699	n/a			
	Spatial (PCNMs)	1.639	0.098	n/a			
FRic	Environment	4.006	0.004	TempSeas	0.178	8.142	0.004
	Biogeography	0.890	0.387	n/a			
	Protected Area	1.259	0.278	n/a			
	Spatial (PCNMs)	3.249	0.022	PCNM4	0.226	10.622	0.008
FDis	Environment	1.093	0.393	n/a			
	Biogeography	0.111	0.947	n/a			
	Protected Area	0.109	0.892	n/a			
	Spatial (PCNMs)	1.378	0.281	n/a			
RaoQ	Environment	1.229	0.321	n/a			
	Biogeography	0.508	0.676	n/a			
	Protected Area	0.244	0.808	n/a			
	Spatial (PCNMs)	1.445	0.221	n/a			
PDm	Environment	8.187	0.001	AnnTemp	0.097	4.561	0.040
	Biogeography	0.414	0.769	n/a			
	Protected Area	2.499	0.099	n/a			
	Spatial (PCNMs)	3.758	0.007	PCNM8	0.223	10.475	0.001
				PCNM7	0.304	4.704	0.035
MNTD	Environment	1.310	0.287	n/a			
	Biogeography	0.638	0.557	n/a			
	Protected Area	1.194	0.302	n/a			
	Spatial (PCNMs)	1.070	0.424	n/a			
NRI	Environment	1.470	0.223	n/a			
	Biogeography	1.308	0.300	n/a			
	Protected Area	0.879	0.424	n/a			
	Spatial (PCNMs)	1.460	0.238	n/a			
Australia							
Alpha	Environment	0.680	0.633	n/a			
	Biogeography	0.701	0.509	n/a			
	Protected Area	3.517	0.028	Area	0.099	6.482	0.008
	Spatial (PCNMs)	0.989	0.461	n/a			

Table 4.9 (continued)

		ANOVA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj.R^2**	***F*-value**	***p*-value**
Comp.	Environment	1.817	0.001	Elevation	0.027	2.381	<0.000
				PrecipSeas	0.043	1.843	0.002
				TempSeas	0.053	1.502	0.023
				AnnTemp	0.071	1.916	0.002
	Biogeography	0.838	0.794	n/a			
	Protected Area	1.592	0.017	Area	0.017	1.881	0.023
	Spatial (PCNMs)	1.431	0.001	PCNM3	0.048	3.541	0.001
				PCNM6	0.069	2.069	0.003
				PCNM5	0.084	1.827	0.012
				PCNM7	0.098	1.640	0.009
Beta[2]	Environment	4.526	0.001	Elevation	0.121	7.904	<0.000
				TempSeas	0.199	5.786	0.002
				PrecipSeas	0.231	2.954	0.039
				AnnTemp	0.264	3.121	0.030
	Biogeography	0.999	0.42	n/a			
	Protected Area	4.500	0.003	Area	0.070	4.750	0.016
				Age	0.123	3.963	0.014
	Spatial (PCNMs)	2.477	0.001	PCNM3	0.148	9.668	0.001
				PCNM7	0.196	3.925	0.017
				PCNM6	0.241	3.835	0.022
				PCNM5	0.272	3.022	0.044
FDis	Environment	0.627	0.645	n/a			
	Biogeography	0.198	0.807	n/a			
	Protected Area	0.489	0.557	n/a			
	Spatial (PCNMs)	1.752	0.101	n/a			
FRic	Environment	2.202	0.063	n/a			
	Biogeography	0.801	0.453	n/a			
	Protected Area	3.281	0.045	Area	0.064	4.428	0.037
	Spatial (PCNMs)	2.589	0.146	n/a			
RaoQ	Environment	0.512	0.764	n/a			
	Biogeography	0.249	0.785	n/a			
	Protected Area	1.327	0.219	n/a			
	Spatial (PCNMs)	2.318	0.036	PCNM7	0.110	7.209	0.011
				PCNM8	0.163	4.106	0.046
PDm	Environment	0.587	0.704	n/a			
	Biogeography	1.310	0.223	n/a			
	Protected Area	2.032	0.138	n/a			
	Spatial (PCNMs)	1.310	0.243	n/a			
MPD	Environment	1.292	0.270	n/a			
	Biogeography	0.217	0.810	n/a			
	Protected Area	1.083	0.322	n/a			
	Spatial (PCNMs)	3.077	0.007	PCNM6	0.186	12.394	0.001
				PCNM3	0.244	4.821	0.032
MNTD	Environment	1.791	0.141	n/a			
	Biogeography	0.103	0.906	n/a			
	Protected Area	5.577	0.006	Area	0.156	10.231	0.003
	Spatial (PCNMs)	1.229	0.292	n/a			

Table 4.9 (continued)

		ANOVA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj.R^2**	***F*-value**	***p*-value**
NRI	Environment	0.952	0.434	n/a			
	Biogeography	0.317	0.730	n/a			
	Protected Area	1.890	0.173	n/a			
	Spatial (PCNMs)	2.024	0.046	PCNM6	0.118	7.711	0.010
				PCNM3	0.220	7.368	0.012

[1] First 3 PCoA axes of the Jaccard index

[2] First 2 PCoA axes of the Jaccard index

Abbreviations: Comp., composition; FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index; AnnTemp, Annual mean temperature; TempSeas, Temperature seasonality; AnnPrecip, Annual mean precipitation; PrecipSeas, Precipitation seasonality; PCNM, Principal Coordinate of Neighbour Matrices; n/a, not applicable because not significant; NS, no variable selected

Table 4.10. Forward selection of variables and RDA results for non-linearly detrended arboreal mammal diversity in Madagascar and Australia.

		ANOVA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj.R^2**	***F*-value**	***p*-value**
Madagascar							
Alpha	Location	6.390	0.005	Longitude	0.270	13.191	0.002
	Environment	4.708	0.005	TempSeas	0.249	11.969	0.002
				AnnPrecip	0.360	6.538	0.015
	Biogeography	0.698	0.548	n/a			
	Protected Area	0.205	0.831	n/a			
	Spatial (PCNMs)	4.041	0.003	PCNM2	0.126	5.779	0.017
				PCNM4	0.246	6.092	0.022
				PCNM1	0.362	6.611	0.025
				PCNM8	0.444	5.460	0.026
Comp.	Location	6.165	0.001	Longitude	0.200	9.216	0.001
				Latitude	0.240	2.689	0.005
	Environment	4.132	<0.000	TempSeas	0.171	7.830	<0.000
				Elevation	0.253	4.512	<0.000
				AnnPrecip	0.300	3.080	<0.000
				AnnTemp	0.315	1.629	0.020
	Biogeography	1.753	0.01	Edge	0.0527	0.287	0.004
	Protected Area	1.164	0.221	n/a			
	Spatial (PCNMs)	2.910	0.001	PCNM2	0.135	6.041	0.001
				PCNM1	0.211	4.180	0.001
				PCNM5	0.260	3.039	0.001
				PCNM6	0.306	3.021	0.001
				PCNM4	0.348	2.867	0.002
				PCNM3	0.371	2.035	0.015
				PCNM7	0.392	1.890	0.015
Beta[1]	Location	33.405	0.001	Longitude	0.661	65.206	0.001
	Environment	29.090	<0.000	TempSeas	0.561	43.207	<0.000
				AnnPrecip	0.798	38.467	<0.000
	Biogeography	1.917	0.131	n/a			
	Protected Area	1.602	0.210	n/a			
	Spatial (PCNMs)	12.79	0.001	PCNM2	0.434	6.311	0.001
				PCNM1	0.636	18.685	0.001
				PCNM5	0.726	11.296	0.003
				PCNM4	0.783	8.795	0.008
FDis	Location	8.459	0.002	Latitude	0.320	16.536	0.001
	Environment	4.983	0.003	Elevation	0.342	18.186	<0.000
	Biogeography	1.283	0.298	n/a			
	Protected Area	0.531	0.586	n/a			
	Spatial (PCNMs)	3.133	0.010	PCNM1	0.281	13.927	0.002
				PCNM4	0.383	6.284	0.019
FDiv	Location	5.874	0.010	Latitude	0.251	12.058	0.001
	Environment	4.279	0.004	Elevation	0.379	21.162	<0.000
	Biogeography	1.684	0.197	n/a			
	Protected Area	0.366	0.674	n/a			
	Spatial (PCNMs)	2.566	0.028	PCNM1	0.219	10.248	0.005
				PCNM4	0.332	6.449	0.020

Table 4.10 (continued)

		ANOVA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj.R^2**	***F*-value**	***p*-value**
FRic	Location	4.784	0.026	Longitude	0.102	4.771	0.042
				Latitude	0.186	4.303	0.043
	Environment	6.118	0.002	TempSeas	0.252	12.142	0.002
				PrecipSeas	0.363	6.550	0.015
	Biogeography	1.072	0.375	n/a			
	Protected Area	1.123	0.349	n/a			
	Spatial (PCNMs)	3.449	0.006	PCNM2	0.161	7.317	0.013
				PCNM5	0.255	5.075	0.038
RaoQ	Location	7.078	0.002	Latitude	0.277	13.645	0.001
	Environment	3.935	0.010	Elevation	0.267	13.028	0.001
				TempSeas	0.341	4.581	0.037
	Biogeography	0.822	0.523	n/a			
	Protected Area	0.357	0.701	n/a			
	Spatial (PCNMs)	3.115	0.015	PCNM1	0.259	12.542	0.002
				PCNM4	0.361	6.119	0.017
				PCNM8	0.432	4.886	0.036
PDm	Location	1.998	0.157	n/a			
	Environment	2.047	0.097	n/a			
	Biogeography	0.567	0.657	n/a			
	Protected Area	4.664	0.020	Age	0.123	5.633	0.028
	Spatial (PCNMs)	3.529	0.011	PCNM8	0.208	9.672	0.002
				PCNM2	0.370	9.200	0.007
				PCNM7	0.471	6.955	0.020
MPD	Location	0.658	0.535	n/a			
	Environment	1.051	0.403	n/a			
	Biogeography	1.004	0.382	n/a			
	Protected Area	0.711	0.513	n/a			
	Spatial (PCNMs)	1.572	0.170	n/a			
MNTD	Location	5.926	0.006	Longitude	0.227	10.692	0.005
	Environment	4.522	0.004	AnnPrecip	0.218	10.209	0.004
	Biogeography	0.802	0.496	n/a			
	Protected Area	1.351	0.295	n/a			
	Spatial (PCNMs)	3.120	0.023	PCNM4	0.128	5.830	0.019
				PCNM1	0.256	6.514	0.021
				PCNM2	0.358	5.957	0.029
NRI	Location	0.445	0.634	n/a			
	Environment	1.024	0.412	n/a			
	Biogeography	0.940	0.448	n/a			
	Protected Area	0.488	0.626	n/a			
	Spatial (PCNMs)	1.756	0.140	n/a			
NTI	Location	2.520	0.104	n/a			
	Environment	2.481	0.056	n/a			
	Biogeography	0.577	0.658	n/a			
	Protected Area	6.440	0.006	NS			
	Spatial (PCNMs)	1.435	0.220	n/a			

Table 4.10 (continued)

		ANOVA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj.R^2**	***F*-value**	***p*-value**
Australia							
Alpha	Location	0.585	0.562	n/a			
	Environment	1.940	0.147	n/a			
	Biogeography	1.940	0.163	n/a			
	Protected Area	2.255	0.117	n/a			
	Spatial (PCNMs)	1.260	0.306	n/a			
Comp.	Location	7.441	<0.000	Longitude	0.143	9.365	0.001
				Latitude	0.205	4.493	0.001
	Environment	3.446	<0.000	AnnTemp	0.238	10.048	<0.000
				AnnPrecip	0.267	2.112	0.022
	Biogeography	2.869	<0.000	Water	0.0545	3.881	<0.000
				Edge	0.070	1.794	0.027
	Protected Area	5.663	0.001	Age	0.218	9.106	<0.000
	Spatial (PCNMs)	2.696	<0.000	PCNM1	0.119	7.785	0.001
				PCNM2	0.200	5.927	0.001
				PCNM3	0.245	3.899	0.001
				PCNM6	0.267	2.358	0.001
				PCNM5	0.286	2.274	0.002
Beta[1]	Location	24.467	<0.000	Latitude	0.486	28.438	0.001
				Longitude	0.618	10.672	0.001
	Environment	5.919	<0.000	AnnPrecip	0.462	25.888	<0.000
	Biogeography	2.855	0.037	NS			
	Protected Area	13.876	<0.000	Age	0.425	22.453	<0.000
				Area	0.470	3.386	0.043
	Spatial (PCNMs)	0.086	<0.000	PCNM1	0.567	38.986	0.001
				PCNM3	0.629	5.655	0.012
FDis	Location	0.254	0.773	n/a			
	Environment	1.728	0.175	n/a			
	Biogeography	2.227	0.135	n/a			
	Protected Area	0.439	0.627	n/a			
	Spatial (PCNMs)	0.520	0.773	n/a			
FDiv	Location	19.182	0.001	Longitude	0.384	19.086	<0.000
				Latitude	0.515	8.562	0.007
	Environment	6.493	<0.000	Elevation	0.384	19.086	<0.000
				AnnPrecip	0.515	8.562	0.007
	Biogeography	8.446	0.006	Water	0.351	16.720	<0.000
	Protected Area	6.426	0.008	Age	0.267	11.589	0.002
	Spatial (PCNMs)	11.593	<0.000	PCNM1	0.571	39.681	0.001
				PCNM6	0.638	6.107	0.021
FRic	Location	1.120	0.346	n/a			
	Environment	0.929	0.495	n/a			
	Biogeography	2.310	0.131	n/a			
	Protected Area	1.756	0.179	n/a			
	Spatial (PCNMs)	1.440	0.212	n/a			
RaoQ	Location	3.041	0.078	n/a			
	Environment	3.257	0.038	AnnTemp	0.295	13.130	<0.000
	Biogeography	1.970	0.173	n/a			
	Protected Area	3.040	0.074	n/a			
	Spatial (PCNMs)	1.134	0.393	n/a			

Table 4.10 (continued)

		ANOVA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj.R^2**	***F*-value**	***p*-value**
PDm	Location	1.429	0.256	n/a			
	Environment	0.824	0.527	n/a			
	Biogeography	5.785	0.015	Water	0.209	8.656	0.006
	Protected Area	0.591	0.583	n/a			
	Spatial (PCNMs)	0.97	0.47	n/a			
MPD	Location	22.146	<0.000	Latitude	0.607	45.928	0.001
	Environment	9.911	<0.000	AnnTemp	0.559	37.781	<0.000
	Biogeography	1.119	0.229	n/a			
	Protected Area	12.978	<0.000	Age	0.430	22.904	<0.000
	Spatial (PCNMs)	4.884	0.008	PCNM1	0.307	13.865	0.001
				PCNM2	0.519	13.299	0.004
MNTD	Location	0.865	0.445	n/a			
	Environment	0.788	0.543	n/a			
	Biogeography	0.580	0.565	n/a			
	Protected Area	2.005	0.169	n/a			
	Spatial (PCNMs)	2.365	0.070	n/a			
NRI	Location	25.040	<0.000	Latitude	0.637	51.934	0.001
	Environment	10.982	<0.000	AnnTemp	0.574	40.170	<0.000
				AnnPrecip	0.640	6.093	0.022
	Biogeography	0.728	0.495	n/a			
	Protected Area	14.678	<0.000	Age	0.424	22.325	<0.000
				Area	0.485	4.355	0.044
	Spatial (PCNMs)	6.789	0.002	PCNM1	0.325	14.971	0.003
				PCNM2	0.588	18.908	0.001
NTI	Location	0.297	0.756	n/a			
	Environment	1.494	0.235	n/a			
	Biogeography	6.600	0.004	Water	0.218	9.072	0.004
	Protected Area	0.721	0.477	n/a			
	Spatial (PCNMs)	1.250	0.328	n/a			

[1] First 3 PCoA axes of the Jaccard index

Abbreviations: Comp., composition; FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index; AnnTemp, Annual mean temperature; TempSeas, Temperature seasonality; AnnPrecip, Annual mean precipitation; PrecipSeas, Precipitation seasonality; PCNM, Principal Coordinate of Neighbour Matrices; n/a, not applicable because not significant; NS, no variable selected

Table 4.11. Forward selection of variables and RDA results for linearly detrended arboreal mammal community diversity in Madagascar and Australia.

		ANOVA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj.R^2**	***F*-value**	***p*-value**
Madagascar							
Alpha	Environment	2.187	0.071	n/a			
	Biogeography	0.067	0.977	n/a			
	Protected Area	0.506	0.597	n/a			
	Spatial (PCNMs)	1.879	0.101	n/a			
Comp.	Environment	1.672	0.002	PrecipSeas	0.051	2.781	<0.000
	Biogeography	1.188	0.146	n/a			
	Protected Area	0.982	0.503	n/a			
	Spatial (PCNMs)	1.615	0.001	PCNM4	0.046	2.596	0.002
				PCNM6	0.091	2.572	0.001
				PCNM2	0.124	2.168	0.006
				PCNM3	0.154	2.056	0.009
Beta[1]	Environment	6.249	0.001	TempSeas	0.352	18.962	<0.000
				AnnTemp	0.417	4.554	0.041
	Biogeography	0.731	0.560	n/a			
	Protected Area	0.446	0.651	n/a			
	Spatial (PCNMs)	1.666	0.147	n/a			
FRic	Environment	4.182	0.008	NS			
	Biogeography	0.092	0.962	n/a			
	Protected Area	1.941	0.139	n/a			
	Spatial (PCNMs)	1.835	0.113	n/a			
FDis	Environment	0.866	0.507	n/a			
	Biogeography	0.489	0.694	n/a			
	Protected Area	0.781	0.456	n/a			
	Spatial (PCNMs)	1.524	0.205	n/a			
FDiv	Environment	0.939	0.469	n/a			
	Biogeography	1.662	0.220	n/a			
	Protected Area	0.499	0.628	n/a			
	Spatial (PCNMs)	1.634	0.175	n/a			
RaoQ	Environment	0.775	0.593	n/a			
	Biogeography	0.312	0.821	n/a			
	Protected Area	0.481	0.600	n/a			
	Spatial (PCNMs)	1.644	0.171	n/a			
MNTD	Environment	1.937	0.127	n/a			
	Biogeography	0.377	0.744	n/a			
	Protected Area	4.291	0.026	Area	0.185	7.195	0.132
	Spatial (PCNMs)	1.654	0.139	n/a			
Australia							
Comp.	Environment	1.200	0.194	n/a			
	Biogeography	0.854	0.668	n/a			
	Protected Area	1.227	0.216	n/a			
	Spatial (PCNMs)	0.912	0.682	n/a			
Beta[1]	Environment	0.564	0.765	n/a			
	Biogeography	0.092	0.971	n/a			
	Protected Area	2.451	0.091	n/a			
	Spatial (PCNMs)	0.639	0.753	n/a			

Table 4.11 (continued)

		ANOVA		Forward selection			
Diversity measure	**Variable group**	***F*-value**	***p*-value**	**Variables**	**Adj.R^2**	***F*-value**	***p*-value**
FDiv	Environment	3.542	0.025	NS			
	Biogeography	6.254	0.006	Water	0.197	8.114	0.008
	Protected Area	0.074	0.845	n/a			
	Spatial (PCNMs)	1.569	0.213	n/a			
MPD	Environment	0.646	0.662	n/a			
	Biogeography	1.674	0.198	n/a			
	Protected Area	0.070	0.931	n/a			
	Spatial (PCNMs)	0.228	0.978	n/a			
NRI	Environment	0.636	0.663	n/a			
	Biogeography	0.728	0.478	n/a			
	Protected Area	0.503	0.643	n/a			
	Spatial (PCNMs)	0.878	0.532	n/a			

[1] First 3 PCoA axes of the Jaccard index

Abbreviations: Comp., composition; FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index; AnnTemp, Annual mean temperature; TempSeas, Temperature seasonality; AnnPrecip, Annual mean precipitation; PrecipSeas, Precipitation seasonality; PCNM, Principal Coordinate of Neighbour Matrices; n/a, not applicable because not significant; NS, no variable selected

Table 4.12. Variation partitioning results for measures of non-detrended diversity for all nonvolant mammals and arboreal mammals in Madagascar and Australia. Beta diversity in Madagascar is measured as the first PCoA axis of the Jaccard index, the first three PCoA axes for Australia. Proportions of variation are expressed as pure variation and total variation in parentheses. Spatial effects are divided into broad and medium scale effects were both broad and medium scale effects were forward selected. Significant pure components of variation are denoted by asterisks: p≤0.05*, p≤0.01**, p≤0.001***

	All Nonvolant Mammals		Arboreal Mammals	
	Madagascar	**Australia**	**Madagascar**	**Australia**
Alpha				
Location	1.4 (41.5)	<0 (42.7)	<0 (26.9)	NT
Environment	8.4* (62.4)	1.9 (36.8)	0.7 (36.7)	NT
Spatial (All)	8.1 (62.8)	3.5 (44.2)	11.2 (44.4)	NT
• Broad	2.6 (51.0)	3.5 (44.2)	3.5 (36.2)	
• Medium	7.8* (6.9)	NT	9.0* (6.3)	
Biogeographic [a]	NT	<0	NT	NT
Environment ∩ Location	<0	2.6	2.9	
Spatial ∩ Location	<0	8.4	0.1	
Environment ∩ Spatial	11.7	<0	7.3	
Explained Variation	69.8	47.6	46.1	0
Composition				
Location	2.0* (25.2)	1.5** (20.5)	1.9 (24.0)	1.2 (34.8)
Environment	6.5** (33.9)	6.7*** (25.5)	6.1** (33.7)	1.9 (26.7)
Spatial (All)	6.3*** (35.3)	5.4*** (28.8)	8.8*** (38.6)	2.8 (37.9)
• Broad	4.4** (30.6)	5.4*** (28.8)	5.7*** (31.9)	2.8 (37.9)
• Medium	3.0** (19.5)	NT	3.8** (4.0)	NT
Biogeographic [a]	<0	<1	<1	<0
Environment ∩ Location	0.7	0.2	0.3	<0
Spatial ∩ Location	2.2	4.7	3.1	10.1
Environment ∩ Spatial	6.5	4.6	8.6	1.3
Explained Variation	44.5	37.3	47.4	40.8
Beta				
Location	2.8* (58.1)	0.9 (53.0)	<0 (66.1)	0.7 (61.8)
Environment	14.2*** (73.5)	9.3*** (61.3)	9.8*** (85.5)	0.2 (46.2)
Spatial (All)	0.9 (67.0)	3.7* (66.0)	1.6 (78.3)	1.9 (62.9)
• Broad	1.1 (63.6)	3.7* (66.0)	1.6 (78.3)	1.9 (62.9)
• Medium	<0 (1.0)	NT	NT	NT
Biogeographic [a]	<0	<0	NT	NT
Environment ∩ Location	<0	0.3	0.7	<0
Spatial ∩ Location	4.8	10.5	01.7	13.9
Environment ∩ Spatial	8.8	10.5	11.0	<0
Explained Variation	82.0	76.5	88.6	62.7

Table 4.12 (continued)

	All Nonvolant Mammals		Arboreal Mammals	
	Madagascar	**Australia**	**Madagascar**	**Australia**
FRic				
Location	0.9 (15.7)	<0 (42.8)	<0 (18.6)	NT
Environment	11.3* (43.0)	5.0* (47.0)	11.7* (36.3)	NT
Spatial (All)	7.3 (38.6)	4.6 (48.9)	<0 (25.5)	NT
• Broad	7.3 (38.6)	4.6 (48.9)	<0 (25.5)	
• Medium	NT	NT	NT	
Biogeographic [a]	NT	<0	NT	NT
Environment ∩ Location	<0	1.8	<0	
Spatial ∩ Location	<0	4.1	1.3	
Environment ∩ Spatial	16.6	2.3	5.2	
Explained Variation	50.9	54.8	34.3	0
FDiv				
Location	NT	NT	<0 (25.1)	<0 (55.6)
Environment	NT	NT	7.2* (37.9)	4.3* (51.5)
Spatial (All)	NT	NT	7.1 (33.2)	8.2* (72.8)
• Broad			7.1 (33.2)	8.2* (72.8)
• Medium			NT	NT
Biogeographic [a]	NT	NT	NT	3.6* (35.1)
Environment ∩ Location			4.6	<0
Spatial ∩ Location			0.1	12.9
Environment ∩ Spatial			3.8	3.9
Explained Variation	0	0	43.2	86.8
FDis				
Location	<0 (18.1)	2.2 (19.2)	<0 (32.0)	NT
Environment	8.4 (26.1)	6.2 (31.0)	1.2 (34.2)	NT
Spatial (All)	14.3* (34.5)	5.7 (32.7)	8.0 (38.3)	NT
• Broad	2.4 (26.3)	<0 (22.7)	8.0 (38.3)	
• Medium	12.8* (6.8)	7.4* (4.9)	NT	
Biogeographic [a]	NT	NT	NT	NT
Environment ∩ Location	<0	<0	5.3	
Spatial ∩ Location	1.4	<0	2.5	
Environment ∩ Spatial	<0	7.2	2.4	
Explained Variation	40.7	38.3	43.6	0
RaoQ				
Location	<0 (22.4)	0.1 (25.8)	<0 (27.7)	NT
Environment	15.9** (28.9)	3.3 (31.5)	0.7 (34.1)	29.5*
Spatial (All)	21.9** (35.5)	10.9* (41.1)	13.6* (43.2)	NT
• Broad	4.7 (24.1)	3.5 (36.0)	4.5 (36.1)	
• Medium	17.3** (10.3)	6.3* (4.2)	9.3* (5.5)	
Biogeographic [a]	NT	NT	NT	NT
Environment ∩ Location	2.7	1.4	4.5	NT
Spatial ∩ Location	3.3	3.4	0.7	NT
Environment ∩ Spatial	<0	5.9	4.5	NT
Explained Variation	52.9	45.9	46.6	29.5

Table 4.12 (continued)

	All Nonvolant Mammals		Arboreal Mammals	
	Madagascar	**Australia**	**Madagascar**	**Australia**
PDm				
Location	0.1 (42.9)	<0 (38.1)	NT	NT
Environment	5.0 (68.5)	0.3 (25.6)	<0 (15.3)	NT
Spatial (All)	4.0 (68.2)	9.5** (47.8)	31.8*** (47.1)	NT
• Broad	<0 (47.4)	9.5** (47.8)	7.5* (15.0)	
• Medium	6.9* (15.1)	NT	28.2** (30.1)	
Biogeographic [a]	NT	<0	NT	20.9*
Environment ∩ Location	<0	1.4	NT	NT
Spatial ∩ Location	0.1	14.4	NT	NT
Environment ∩ Spatial	20.7	0.6	15.3	NT
Explained Variation	72.6	48.4	47.1	20.9
MPD				
Location	NT	3.7* (16.1)	NT	0.7 (60.8)
Environment	NT	6.2* (26.0)	NT	<0 (55.9)
Spatial (All)	NT	24.8** (43.8)	NT	<0 (51.9)
• Broad		24.8** (43.8)		<0 (51.9)
• Medium		NT		NT
Biogeographic [a]	NT	NT	NT	NT
Environment ∩ Location		<0		6.7
Spatial ∩ Location		<0		3.0
Environment ∩ Spatial		2.4		<0
Explained Variation	0	49.5	0	58.2
MNTD				
Location	<0 (31.1)	2.9 (10.1)	<0 (22.8)	NT
Environment	2.9 (37.6)	6.9* (14.1)	0.1 (30.4)	NT
Spatial (All)	<0 (33.0)	NT	5.8 (35.8)	NT
• Broad	<0 (33.0)		5.8 (35.8)	
• Medium	NT		NT	
Biogeographic [a]	NT	NT	NT	NT
Environment ∩ Location	0.8	7.2	0.6	
Spatial ∩ Location	1.3	NT	0.4	
Environment ∩ Spatial	2.7	NT	5.6	
Explained Variation	34.6	17.0	34.3	0
NRI				
Location	NT	<0 (33.0)	NT	<0 (63.7)
Environment	14.9*	7.0* (41.4)	NT	1.0 (64.0)
Spatial (All)	NT	6.0* (40.3)	NT	0.5 (58.8)
• Broad		6.0* (40.3)		0.5 (58.8)
• Medium		NT		NT
Biogeographic [a]	NT	NT	NT	NT
Environment ∩ Location		<0		6.7
Spatial ∩ Location		<0		2.1
Environment ∩ Spatial		<0		0.2
Explained Variation	14.9	45.5	0	65.4

Table 4.12 (continued)

	All Nonvolant Mammals		Arboreal Mammals	
	Madagascar	**Australia**	**Madagascar**	**Australia**
NTI				
Location	<0 (28.3)	NT	NT	NT
Environment	1.2 (32.3)	NT	NT	NT
Spatial (All)	1.7 (23.0)	NT	NT	NT
• Broad	<0 (11.9)			
• Medium	1.6 (10.5)			
Biogeographic [a]	NT	NT	NT	21.8**
Environment ∩ Location	14.2			NT
Spatial ∩ Location	4.4			NT
Environment ∩ Spatial	5.6			NT
Explained Variation	36.8	0	0	21.8

[a] Not tested as part of model because variation partitioning can only have a maximum of four explanatory matrices, and in the overall global RDA model biogeographic processes' contribution to variation in composition was minor.

Abbreviations: FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index; ∩: indicates the component of shared variation between two sets of explanatory variables (i.e. effect types); NT: not tested because no significant forward selected variables were present.

Table 4.13. Variation partitioning results for measures of detrended diversity for all nonvolant mammals and arboreal mammals in Madagascar and Australia. Beta diversity in Madagascar is measured as the first PCoA axis of the Jaccard index, the first three PCoA axes for Australia. Proportions of variation are expressed as pure variation and total variation in parentheses. Spatial effects are divided into broad and medium scale effects were both broad and medium scale effects were forward selected. Significant pure components of variation are denoted by asterisks: p≤0.05*, p≤0.01**, p≤0.001***

	All Nonvolant Mammals		Arboreal Mammals	
	Madagascar	**Australia**	**Madagascar**	**Australia**
Alpha				
Environment	2.6* (3.6)	NT	NT	n/a
Spatial (All)	3.2** (3.9)	NT	NT	
• Broad	2.9**(0.2)			
• Medium	0.4 (10.4)			
Biogeographic	NT	NT	NT	
Environment ∩ Spatial	1.0			
Explained Variation	6.9	0	0	
Composition				
Environment	2.4* (5.1)	3.8*** (7.1)	2.3* (5.1)	NT
Spatial (All)	5.5** (7.5)	5.2*** (9.8)	12.6*** (10.4)	NT
• Broad	5.5** (7.5)	5.2*** (9.8)	8.6*** (10.4)	
• Medium	2.1* (2.0)	NT	4.3*** (4.2)	
Biogeographic	NT	NT	NT	NT
Environment ∩ Spatial	2.7	<0	2.8	
Explained Variation	12.4	15.4	17.7	0
Beta				
Environment	17.3**	12.6*** (26.4)	41.7***	NT
Spatial (All)	NT	14.4** (28.2)	NT	NT
• Broad		14.4** (28.2)		
• Medium		NT		
Biogeographic	NT	NT	NT	NT
Environment ∩ Spatial		13.8		
Explained Variation	17.3	40.8	41.7	0
FRic				
Environment	2.5** (3.6)	NT	NT	n/a
Spatial (All)	2.8** (3.9)	NT	NT	
• Broad	2.8** (3.9)			
• Medium	NT			
Biogeographic		NT	NT	
Environment ∩ Spatial	1.1			
Explained Variation	6.4	0	0	

Table 4.13 (continued)

	All Nonvolant Mammals		Arboreal Mammals	
	Madagascar	**Australia**	**Madagascar**	**Australia**
FDiv				
Environment	n/a	n/a	NT	NT
Spatial (All)			NT	NT
• Broad				
• Medium				
Biogeographic			NT	19.7**
Environment ∩ Spatial				
Explained Variation			0	19.7**
FDis				
Environment	NT	NT	NT	n/a
Spatial (All)	NT	NT	NT	
• Broad				
• Medium				
Biogeographic	NT	NT	NT	
Environment ∩ Spatial				
Explained Variation	0	0	0	
RaoQ				
Environment	NT	NT	NT	n/a
Spatial (All)	NT	16.3	NT	
• Broad		11.4* (11.0)		
• Medium		5.3* (16.3)		
Biogeographic	NT	NT	NT	
Environment ∩ Spatial				
Explained Variation	0	16.3	0	
PDm				
Environment	2.7* (3.6)	NT	n/a	n/a
Spatial (All)	3.2* (4.2)	NT		
• Broad	3.2* (4.2)			
• Medium	NT			
Biogeographic	NT	NT		
Environment ∩ Spatial	0.9			
Explained Variation	6.9	0		
MPD				
Environment	n/a	NT	n/a	NT
Spatial (All)		24.4*		NT
• Broad		24.4*		
• Medium		NT		
Biogeographic		NT		NT
Environment ∩ Spatial				
Explained Variation		24.4		0

Table 4.13 (continued)

	All Nonvolant Mammals		Arboreal Mammals	
	Madagascar	**Australia**	**Madagascar**	**Australia**
MNTD				
Environment	NT	NT	NT	n/a
Spatial (All)	NT	NT	NT	
• Broad				
• Medium				
Biogeographic Environment ∩ Spatial	NT	NT	NT	
Explained Variation	0	0	0	
NRI				
Environment	NT	NT	n/a	NT
Spatial (All)	NT	22.4*		NT
• Broad		22.4*		
• Medium				
Biogeographic Environment ∩ Spatial	NT	NT		NT
Explained Variation	0	22.4		0
NTI				
Environment	n/a	n/a	n/a	n/a
Spatial (All)				
• Broad				
• Medium				
Biogeographic Environment ∩ Spatial				
Explained Variation				

Abbreviations: FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index; ∩: indicates the component of shared variation between two sets of explanatory variables (i.e. effect types); NT: not tested because no significant forward selected variables were present

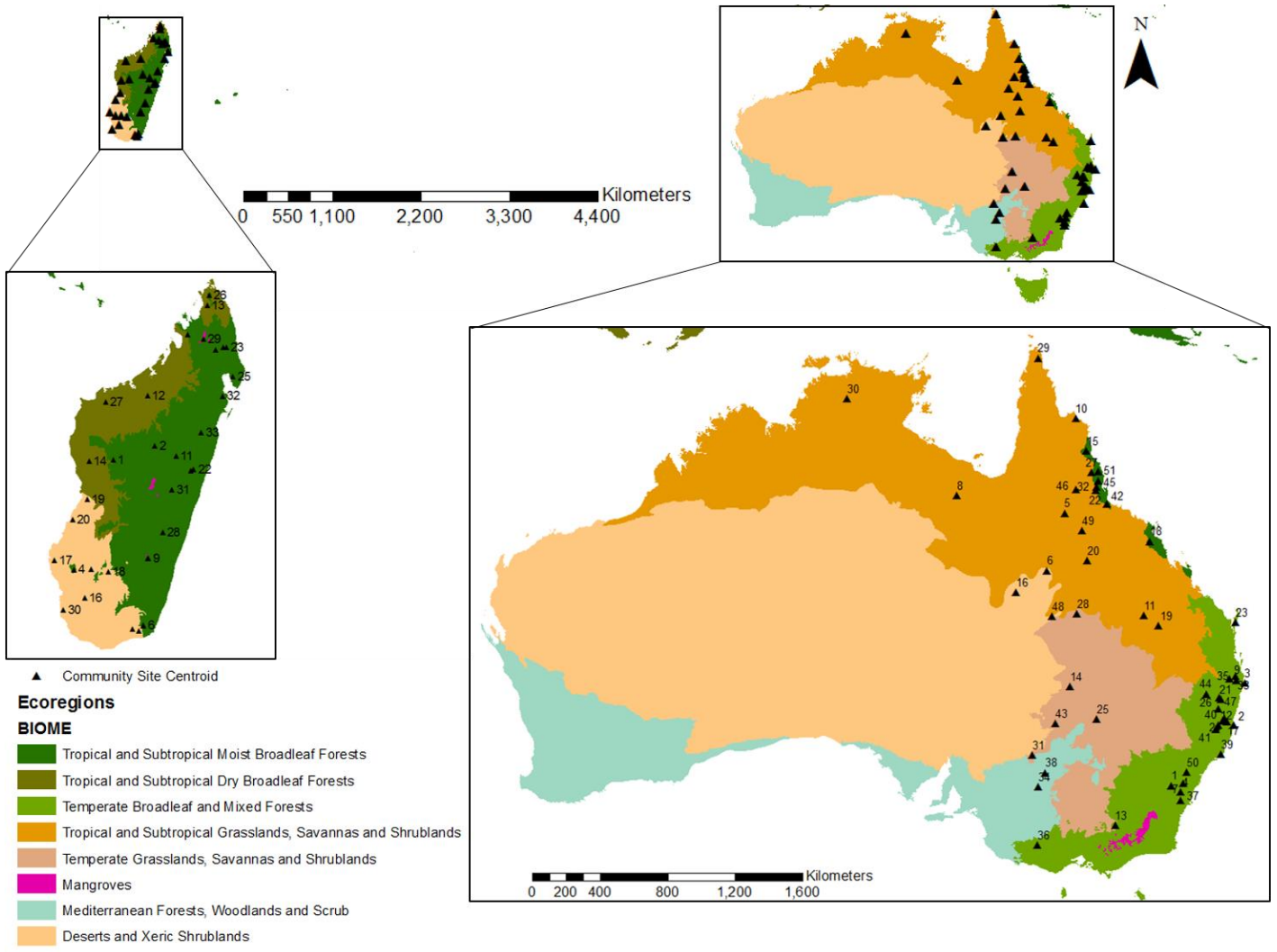


Figure 4.1. Protected area sites in Madagascar and Australia included in this study. Shaded areas depict ecofloristic regions (*sensu* Olson et al. 2001). See Table A.1 and A.2 for index to sites.

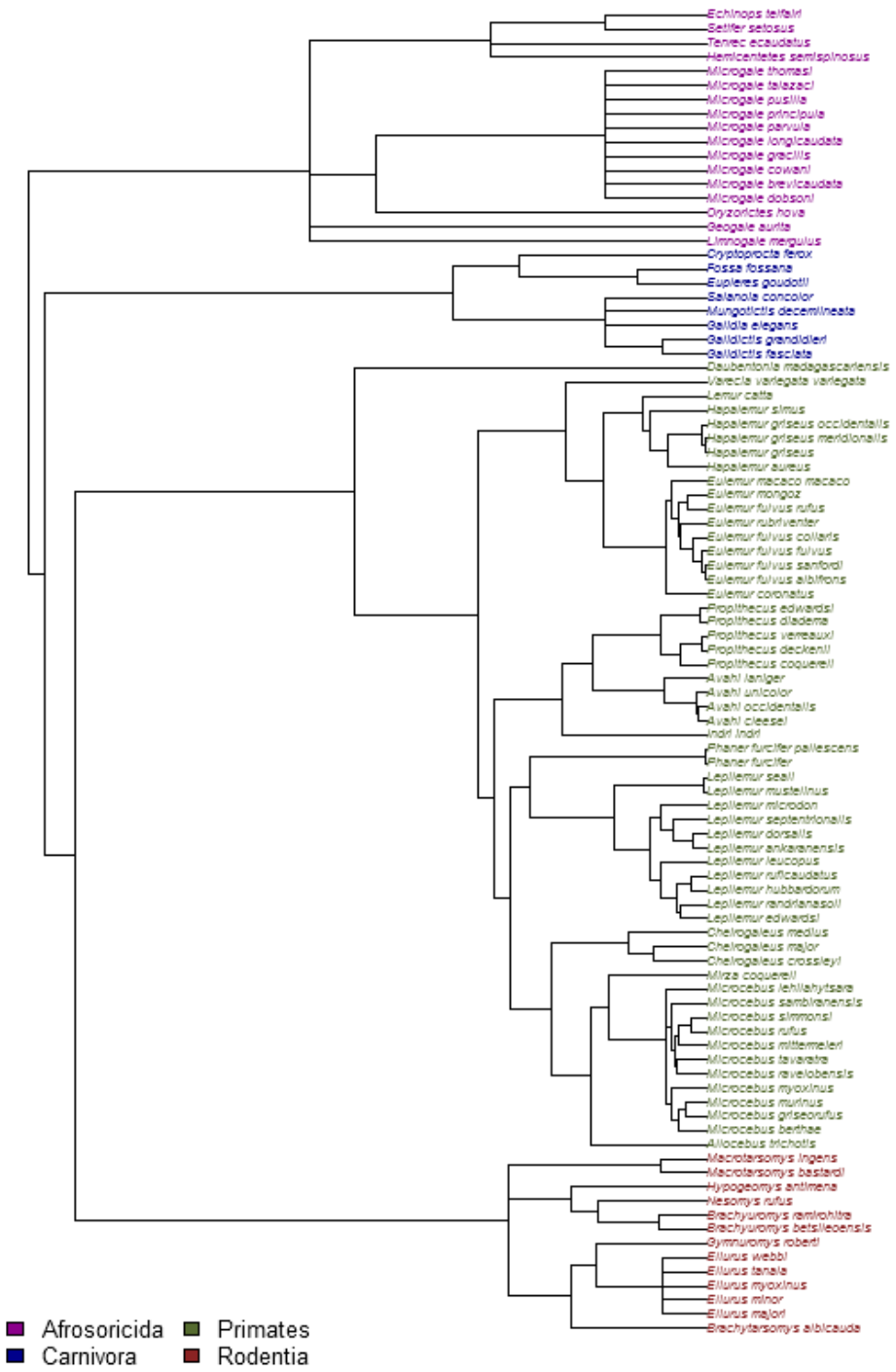


Figure 4.2.A Phylogenetic tree for Madagascar's nonvolant mammals. Mammal branching patterns are after Bininda-Emonds et al. (2007), and primate branching patterns are after Arnold et al. (2010).

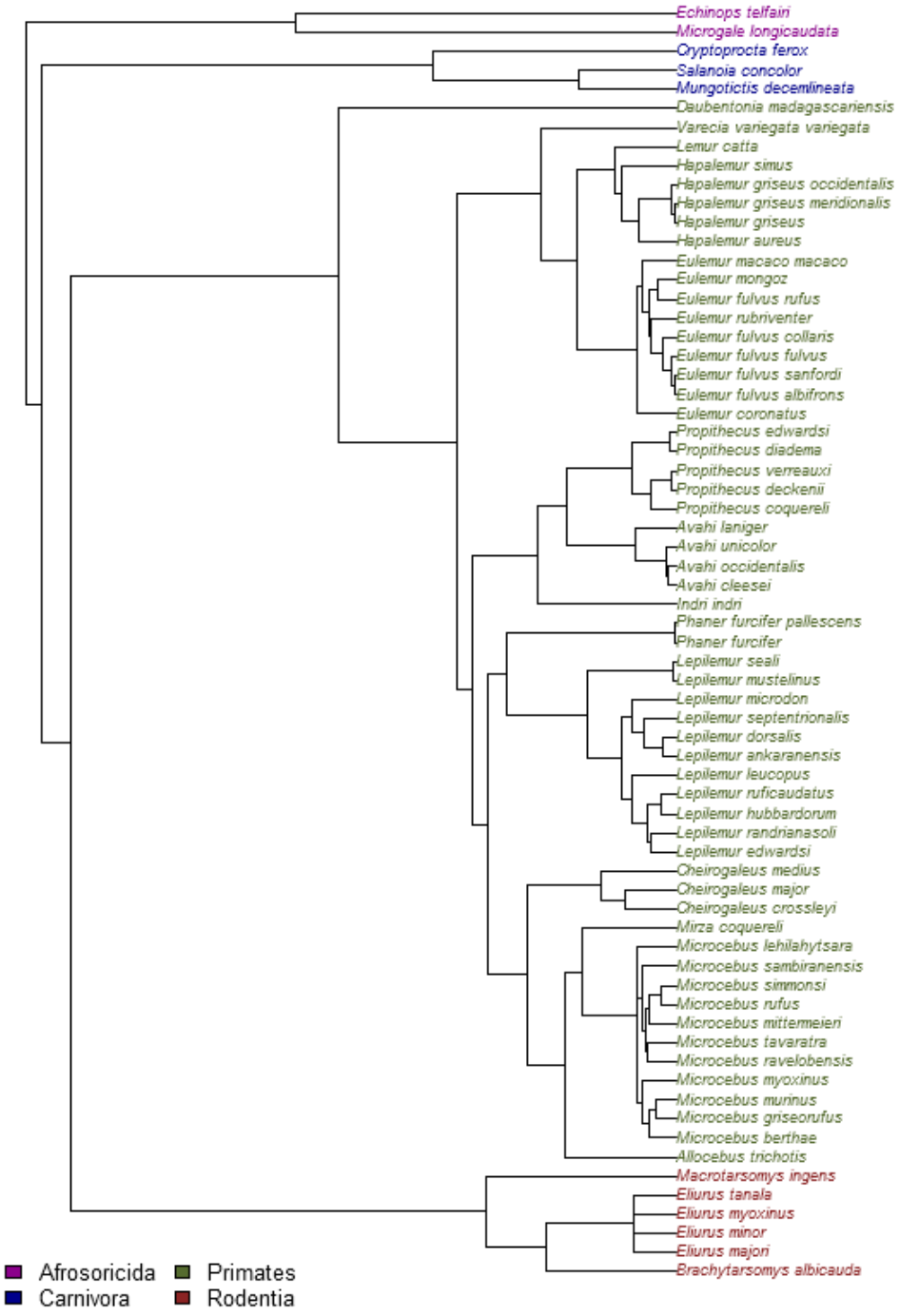


Figure 4.2.B. Phylogenetic tree for Madagascar's arboreal mammals. Mammal branching patterns are after Bininda-Emonds et al. (2007), and primate branching patterns are after Arnold et al. (2010).

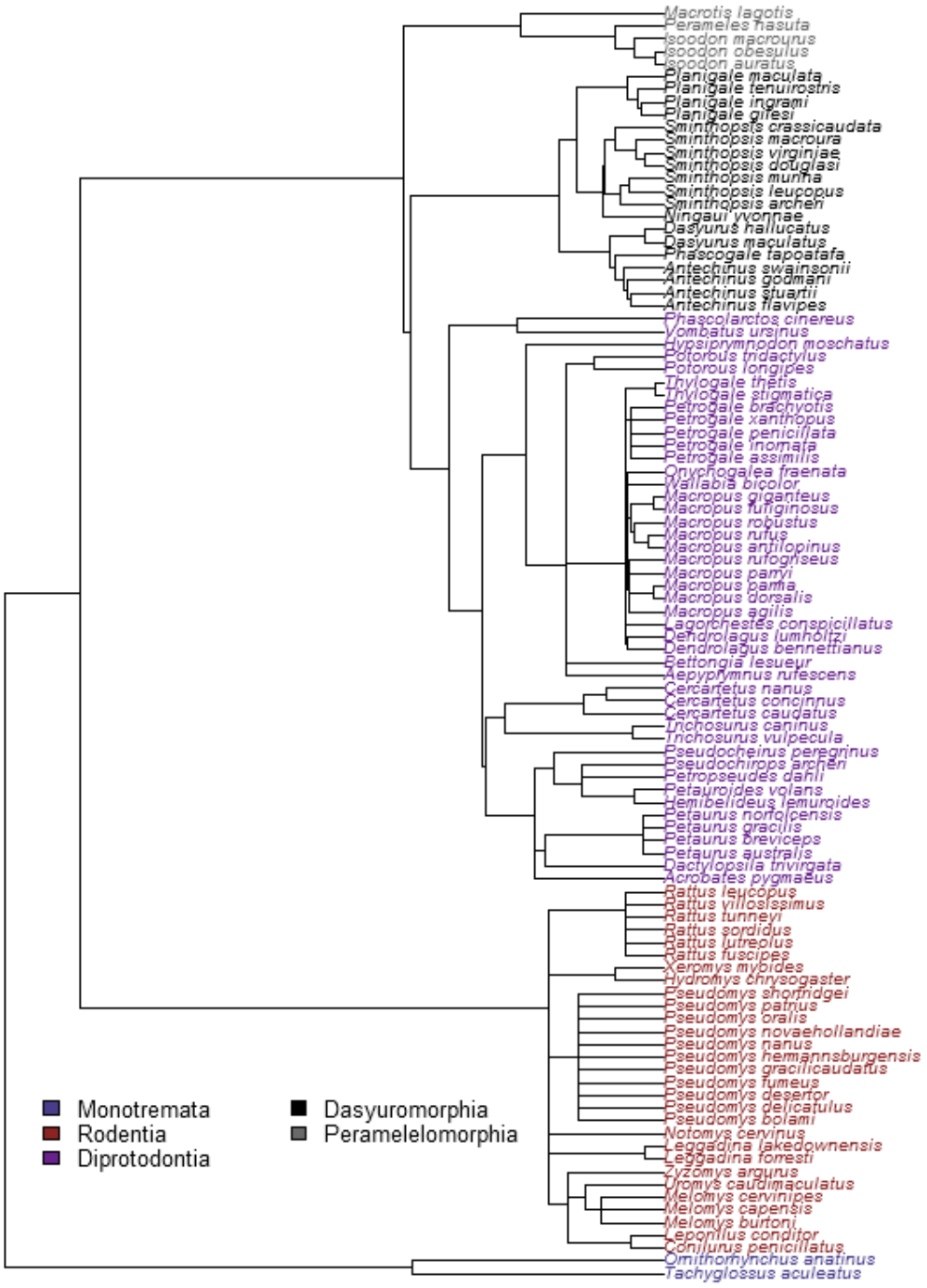


Figure 4.2.C. Phylogenetic tree for Australia's nonvolant mammals. Mammal branching patterns are after Bininda-Emonds et al. (2007).

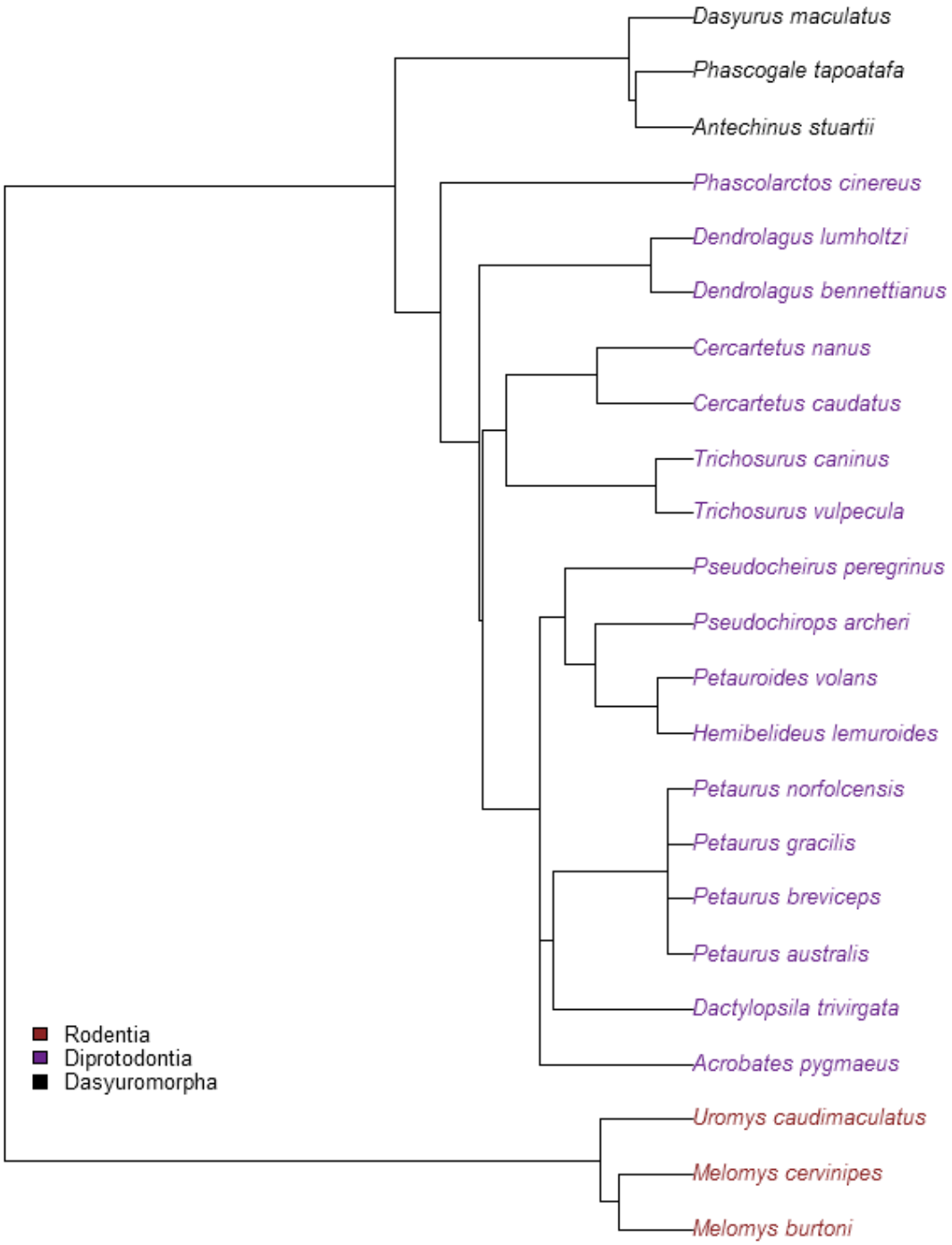


Figure 4.2.D. Phylogenetic tree for Australia's arboreal mammals. Mammal branching patterns are after Bininda-Emond*s* et al. (2007).

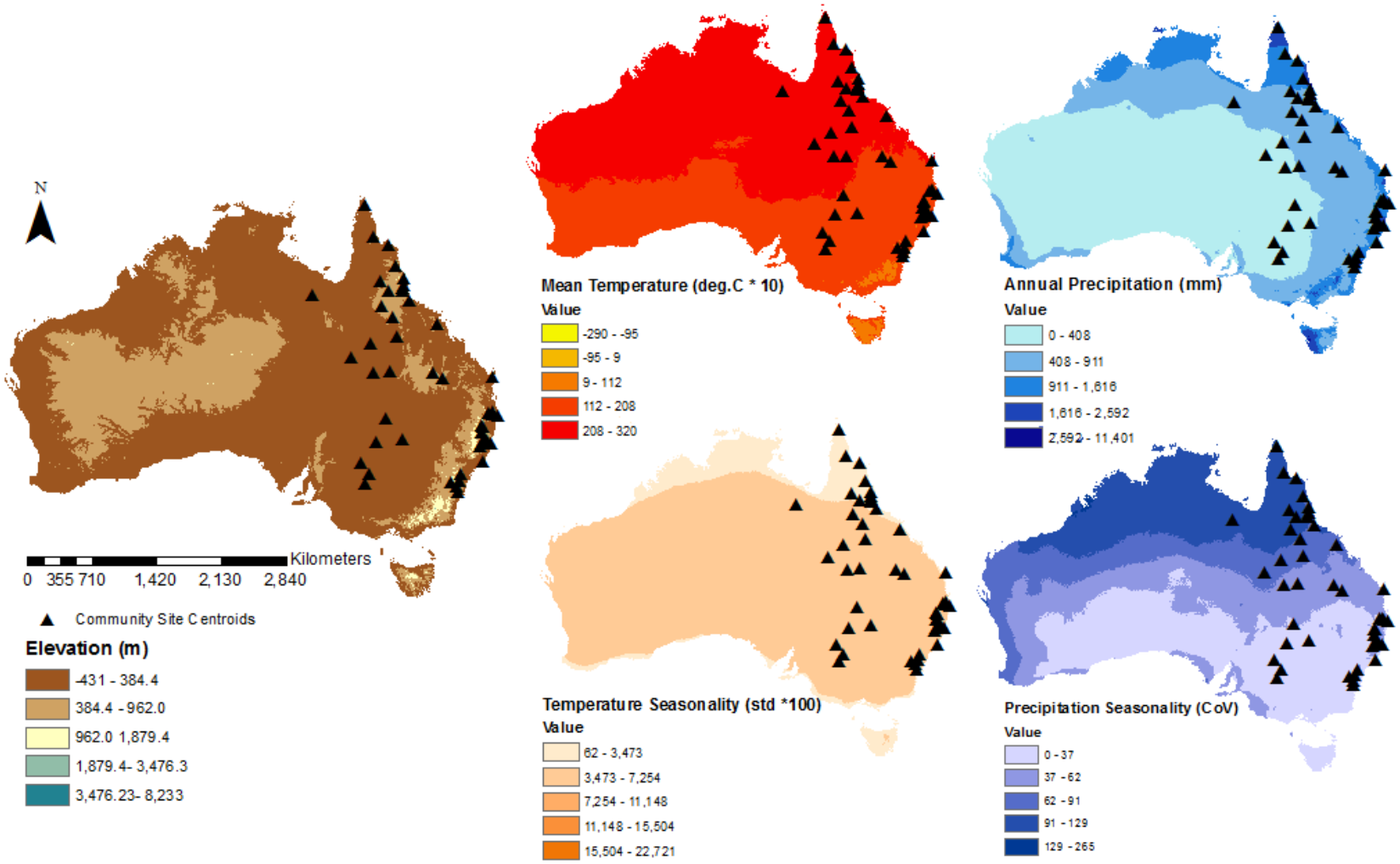
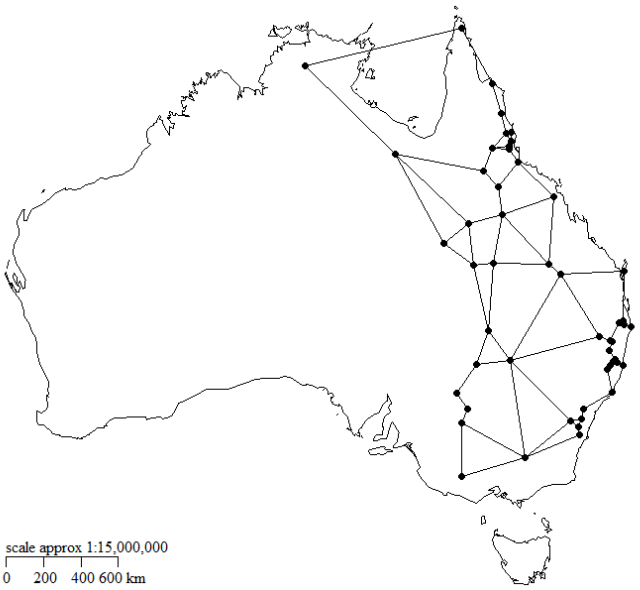


Figure 4.3. Environmental variables across Australia. Values are divided by natural breaks (Jenks) for visual clarity.

(A)



(B)

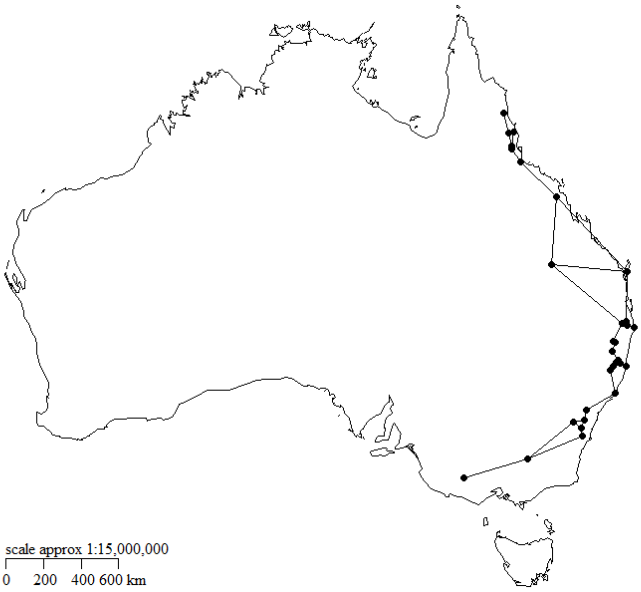


Figure 4.4. The neighbouring graph of study sites for Australia's (A) nonvolant mammal communities, and (B) arboreal mammal communities. Depicts the Euclidean minimum spanning tree of study sites such that the total length of the lines connecting sites is minimized and any site can be reached from any other site by following the lines.

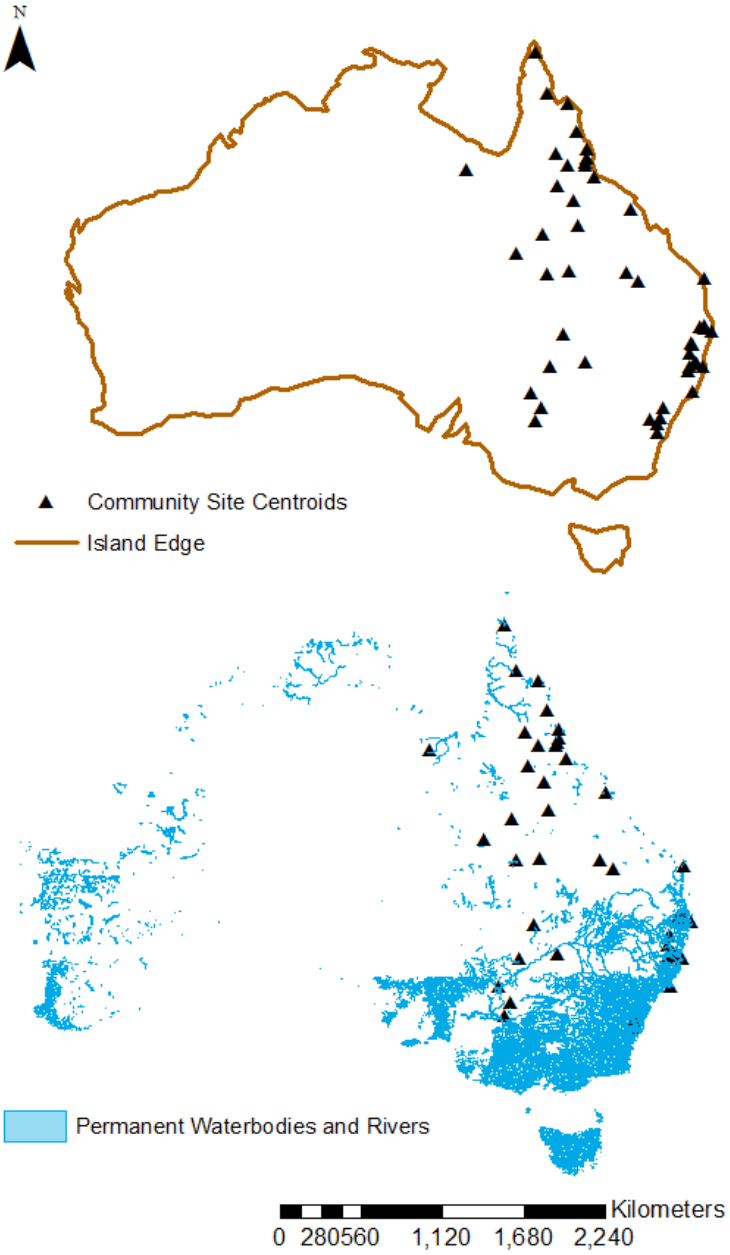
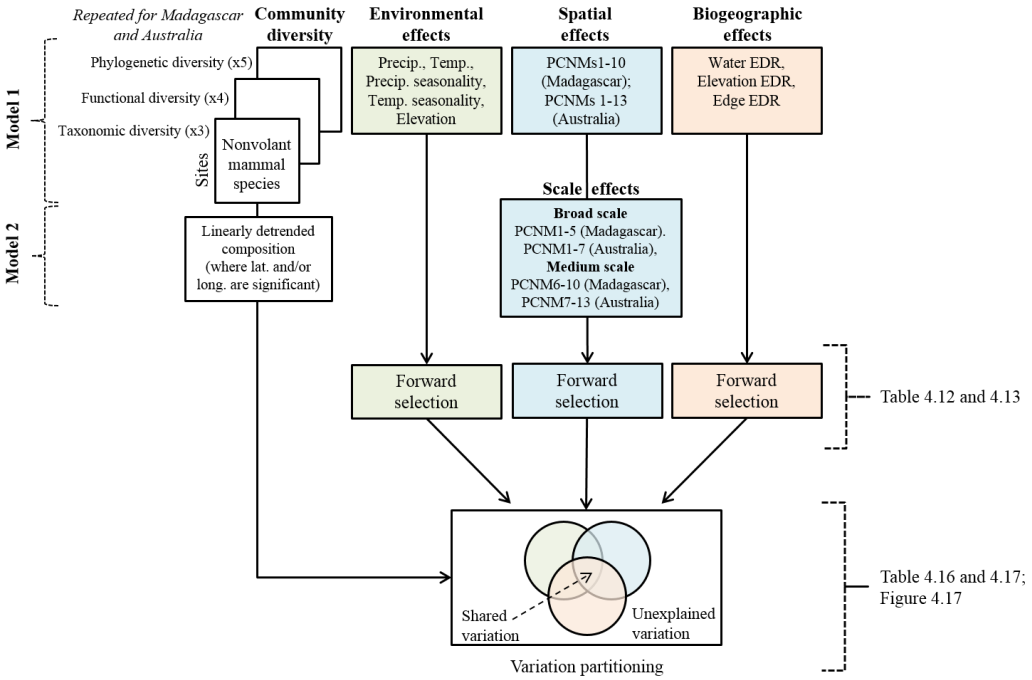


Figure 4.5. Biogeographic features in Australia incorporated into the analysis.

(A)



(B)

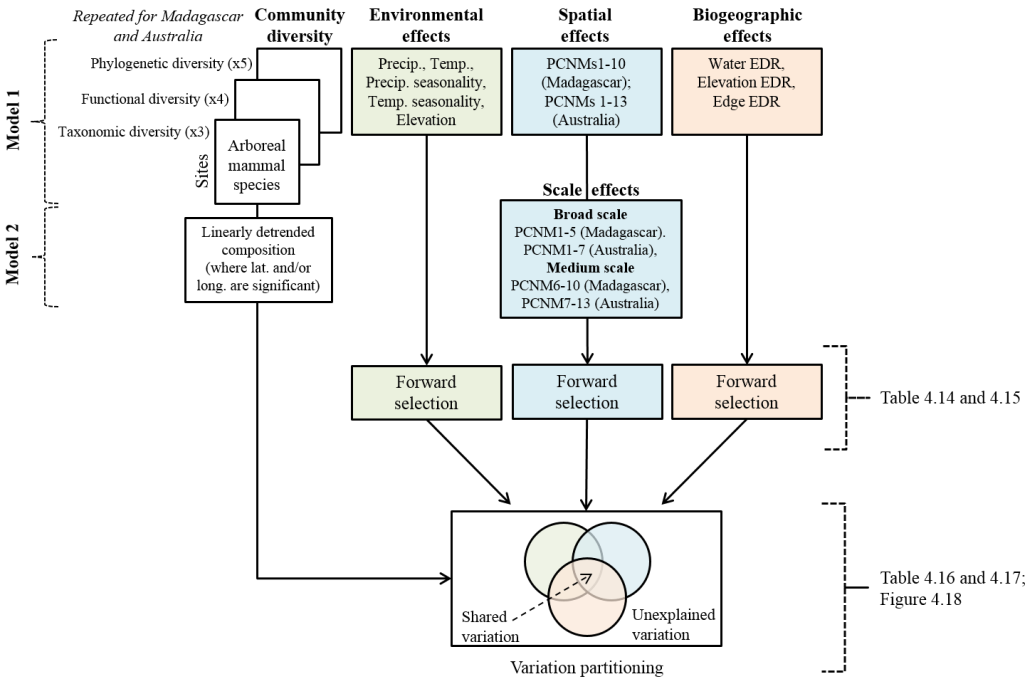


Figure 4.6. Schematic of the different datasets used and the analytical steps performed in this chapter to identify the community assembly processes shaping (A) nonvolant mammal communities, and (B) arboreal mammal communities in Madagascar and Australia. Steps were repeated for each unique diversity measure describing each community. Results of analyses are provided in indicated tables and figures. This schematic is based on Figure 1.6, the analytical framework for the dissertation.

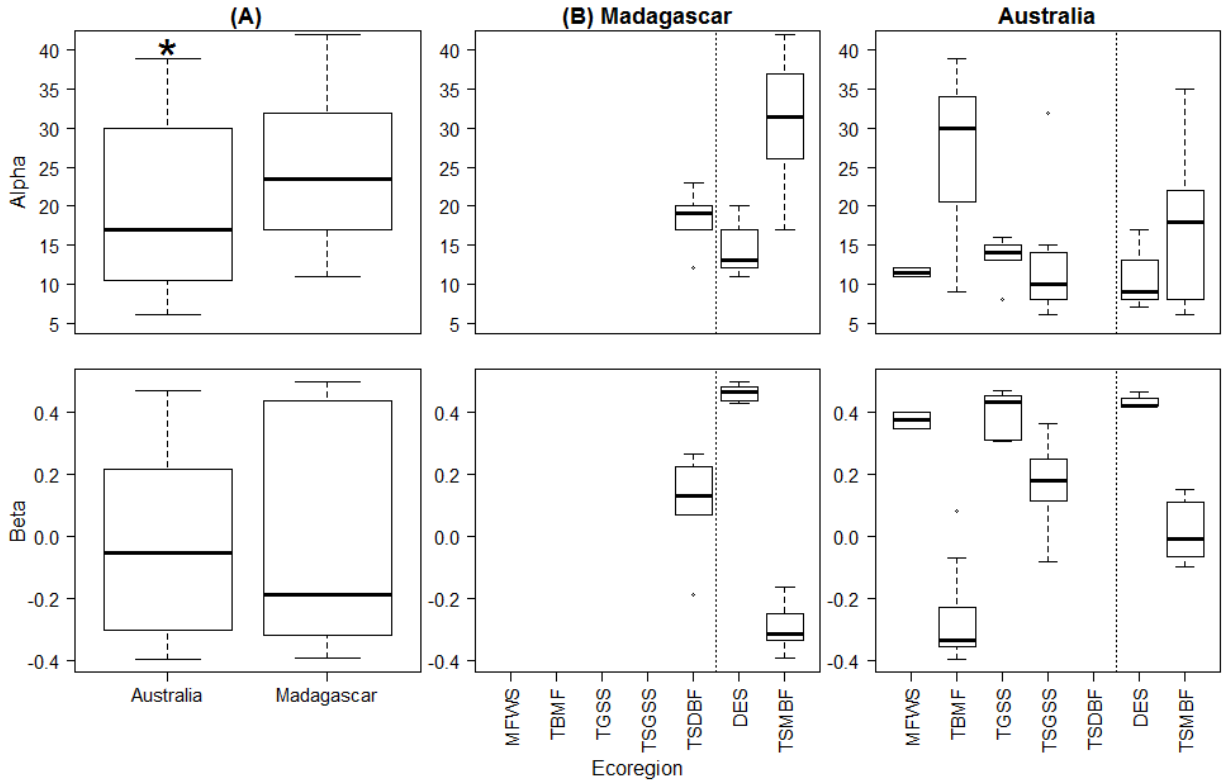


Figure 4.7. Nonvolant mammal taxonomic community diversity compared across (A) Madagascar and Australia, and (B) between ecoregions in Madagascar and Australia. DES and TSMBF are in both Madagascar and Australia, and separated from non-shared ecoregions with a dotted line for clarity. Significant differences between Madagascar and Australia (t-test) are indicated by asterisks: $p < 0.001$***, $p < 0.01$**, $p < 0.05$*. MFWS, Mediterranean forests, woodlands, and scrub; TBMF, temperate broadleaf and mixed forests; TGSS, temperate grasslands, savannahs, and shrublands; TSGSS, tropical and subtropical grasslands, savannahs, and shrublands; TSDBF, tropical and subtropical dry broadleaf forests; DES, deserts and xeric shrublands; TSMBF, tropical and subtropical moist broadleaf forests.

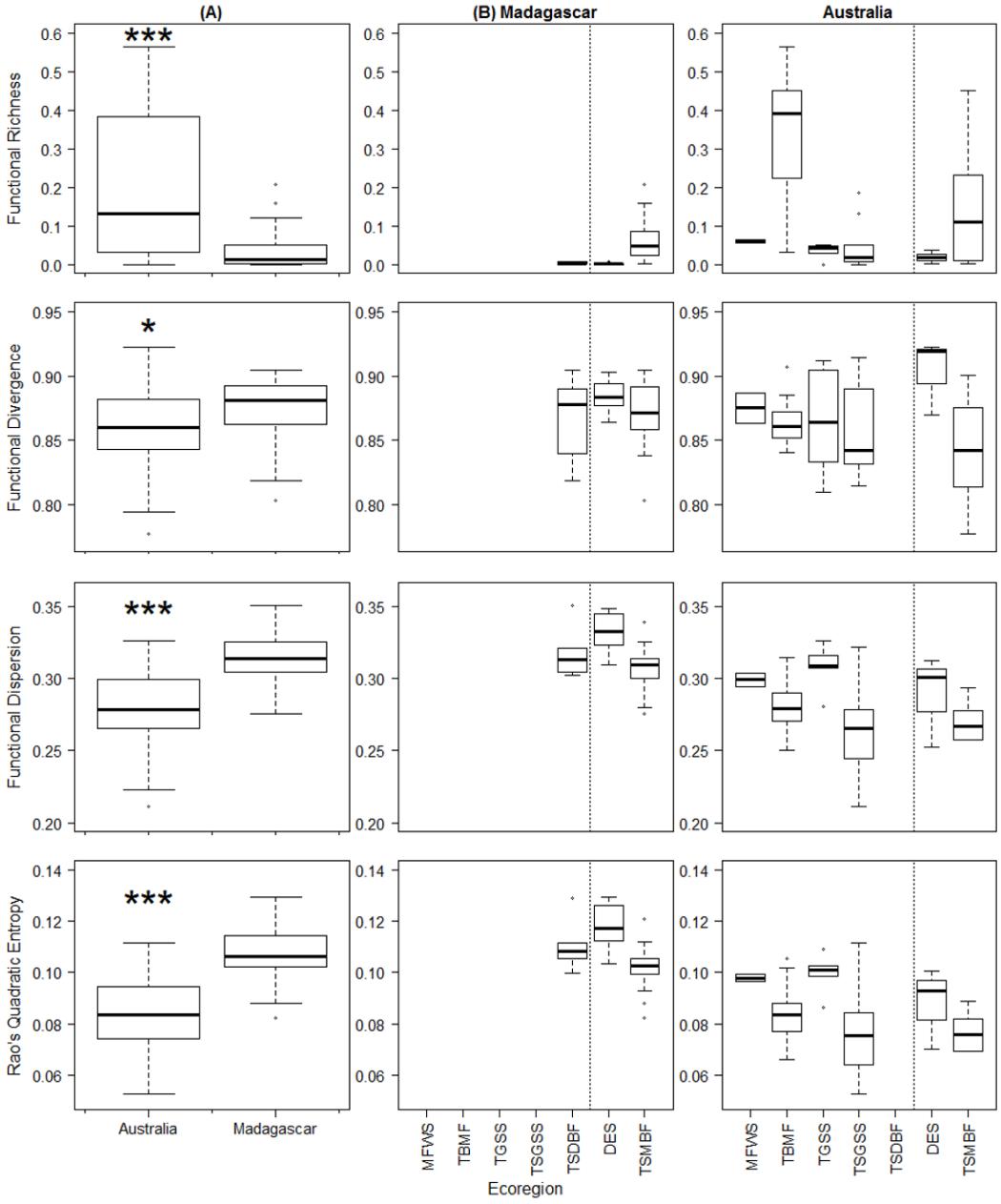


Figure 4.8. Nonvolant mammal functional community diversity compared across (A) Madagascar and Australia, and (B) between ecoregions in Madagascar and Australia. DES and TSMBF are in both Madagascar and Australia, and separated from non-shared ecoregions with a dotted line for clarity. Significant differences between Madagascar and Australia (t-test) are indicated by asterisks: $p < 0.001$***, $p < 0.01$**, $p < 0.05$*. MFWS, Mediterranean forests, woodlands, and scrub; TBMF, temperate broadleaf and mixed forests; TGSS, temperate grasslands, savannahs, and shrublands; TSGSS, tropical and subtropical grasslands, savannahs, and shrublands; TSDBF, tropical and subtropical dry broadleaf forests; DES, deserts and xeric shrublands; TSMBF, tropical and subtropical moist broadleaf forests.

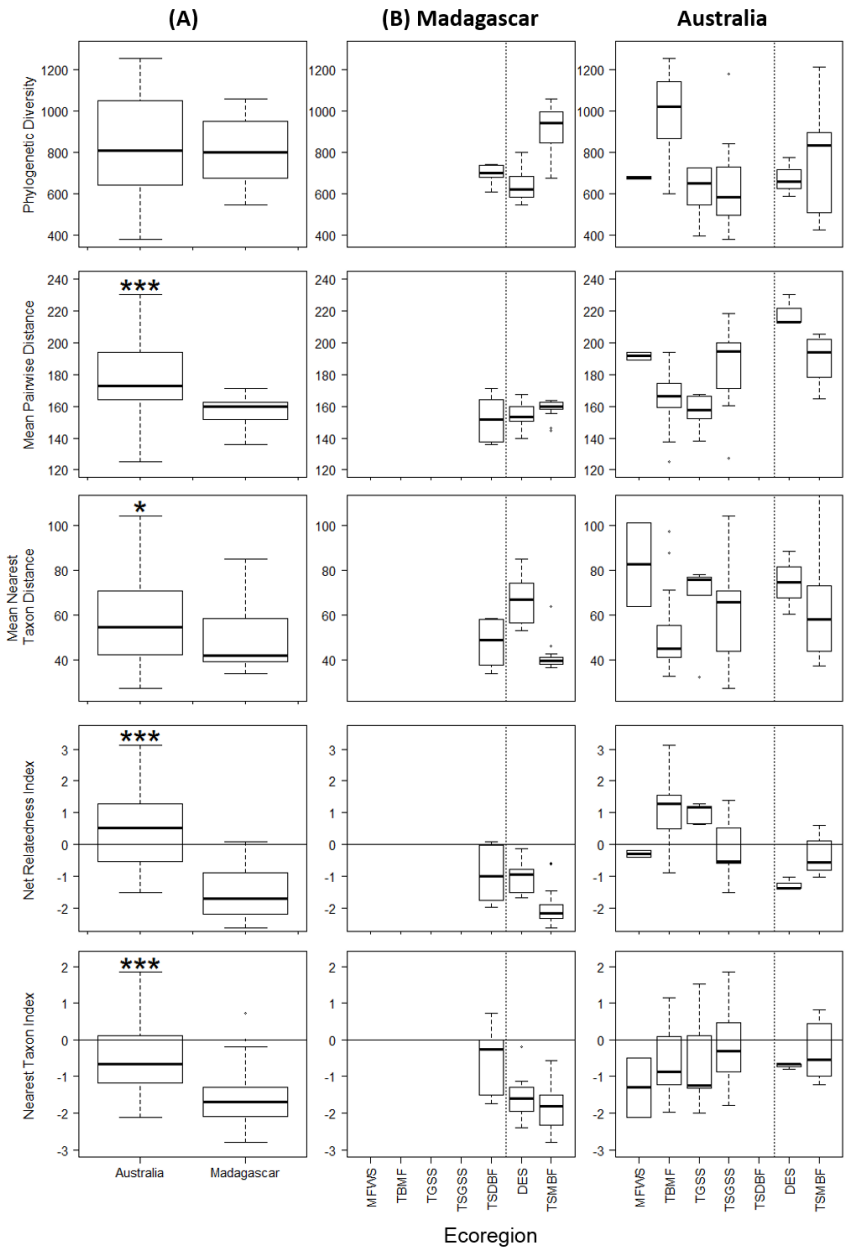


Figure 4.9. Nonvolant mammal phylogenetic community diversity compared across (A) Madagascar and Australia, and (B) between ecoregions in Madagascar and Australia. DES and TSMBF are in both Madagascar and Australia, and separated from non-shared ecoregions with a dotted line for clarity. Horizontal lines are used to emphasize the zero line. Significant differences between Madagascar and Australia (t-test) are indicated by asterisks: $p < 0.001$***, $p < 0.01$**, $p < 0.05$*. MFWS, Mediterranean forests, woodlands, and scrub; TBMF, temperate broadleaf and mixed forests; TGSS, temperate grasslands, savannahs, and shrublands; TSGSS, tropical and subtropical grasslands, savannahs, and shrublands; TSDBF, tropical and subtropical dry broadleaf forests; DES, deserts and xeric shrublands; TSMBF, tropical and subtropical moist broadleaf forests.

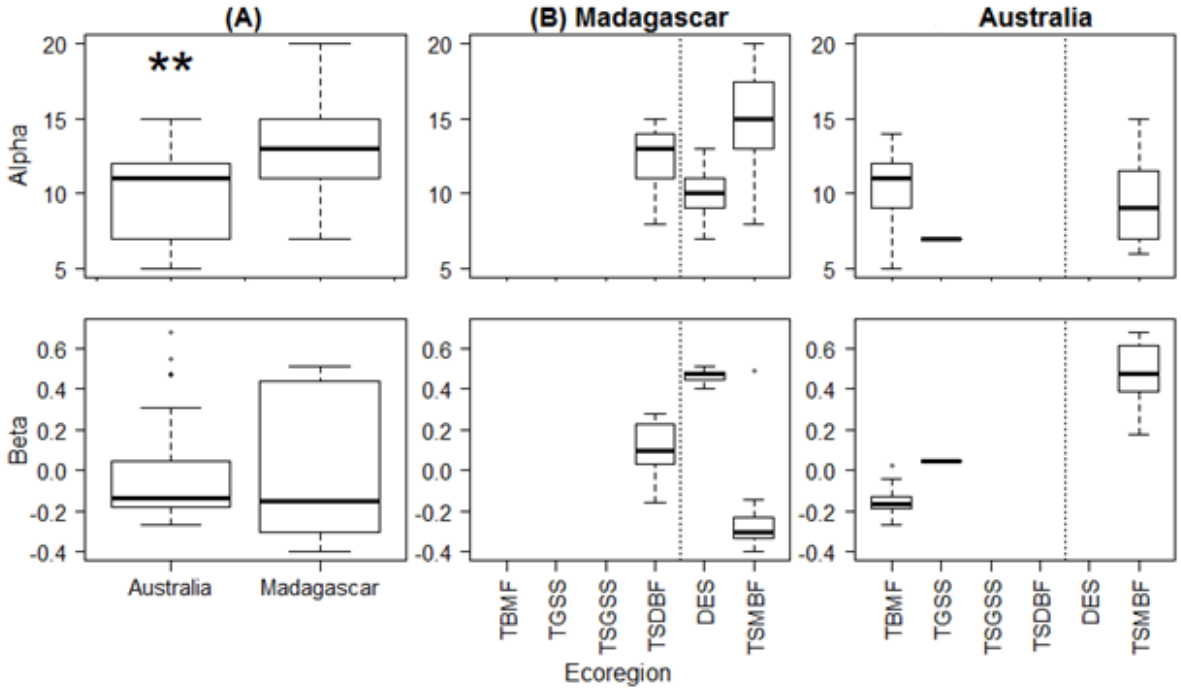


Figure 4.10. Arboreal mammal taxonomic community diversity compared across (A) Madagascar and Australia, and (B) between ecoregions in Madagascar and Australia. DES and TSMBF are in both Madagascar and Australia, and separated from non-shared ecoregions with a dotted line for clarity. Significant differences between Madagascar and Australia (t-test) are indicated by asterisks: $p < 0.001$***, $p < 0.01$**, $p < 0.05$*. TBMF, temperate broadleaf and mixed forests; TGSS, temperate grasslands, savannahs, and shrublands; TSGSS, tropical and subtropical grasslands, savannahs, and shrublands; TSDBF, tropical and subtropical dry broadleaf forests; DES, deserts and xeric shrublands; TSMBF, tropical and subtropical moist broadleaf forests.

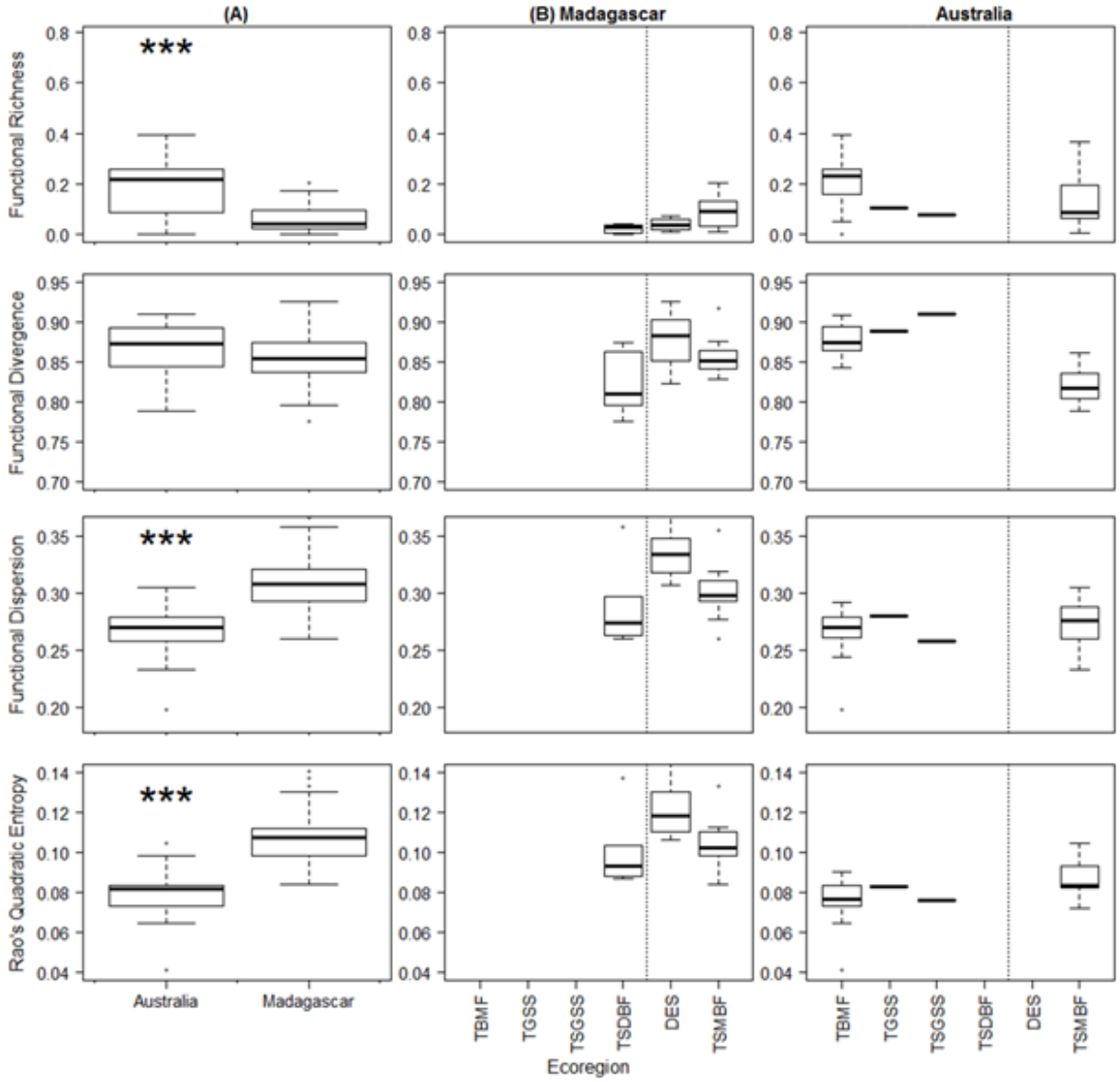


Figure 4.11. Arboreal mammal functional community diversity compared across (A) Madagascar and Australia, and (B) between ecoregions in Madagascar and Australia. DES and TSMBF are in both Madagascar and Australia, and separated from non-shared ecoregions with a dotted line for clarity. Significant differences between Madagascar and Australia (t-test) are indicated by asterisks: $p < 0.001$***, $p < 0.01$**, $p < 0.05$*. TBMF, temperate broadleaf and mixed forests; TGSS, temperate grasslands, savannahs, and shrublands; TSGSS, tropical and subtropical grasslands, savannahs, and shrublands; TSDBF, tropical and subtropical dry broadleaf forests; DES, deserts and xeric shrublands; TSMBF, tropical and subtropical moist broadleaf forests.

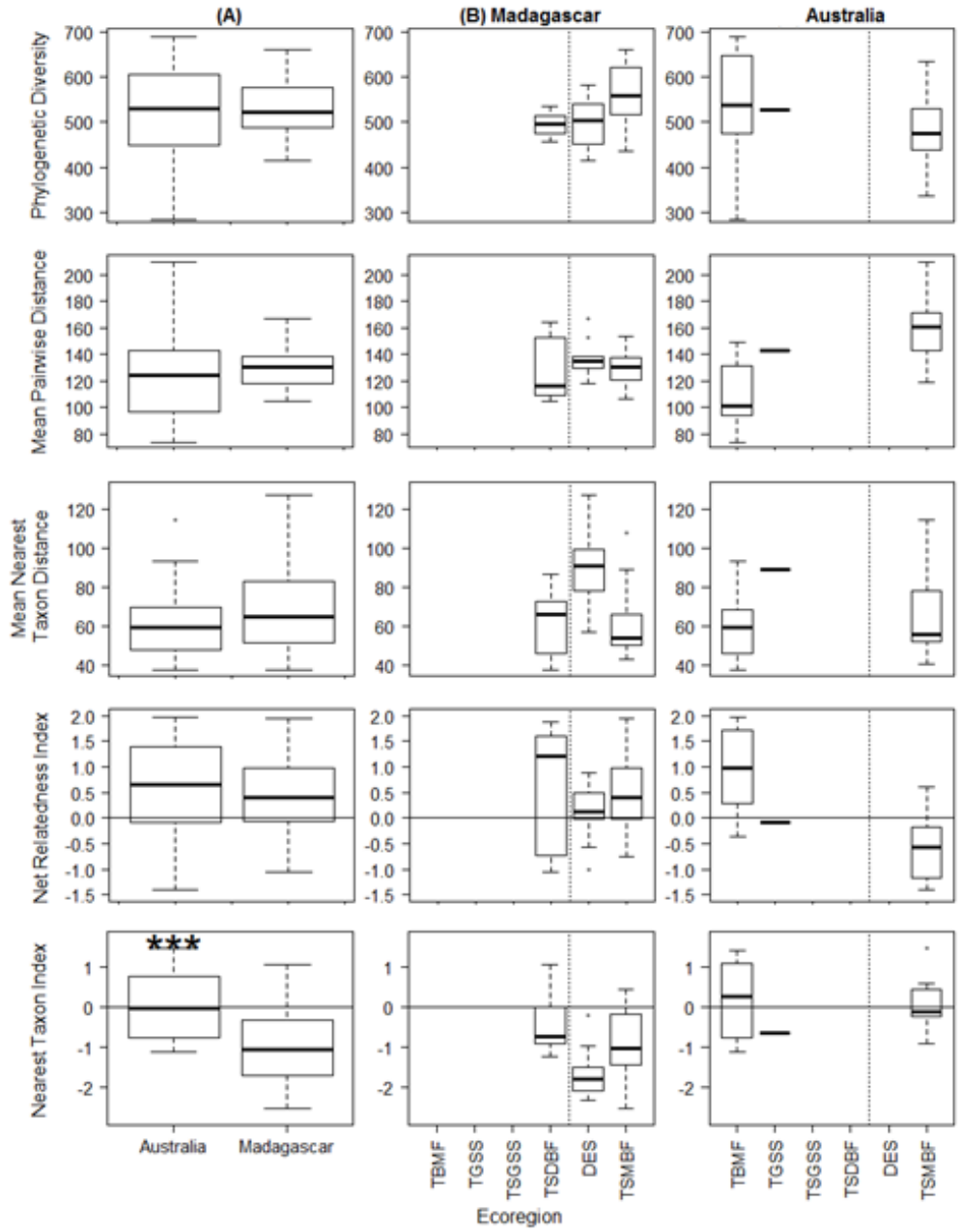


Figure 4.12. Arboreal mammal phylogenetic community diversity compared across (A) Madagascar and Australia, and (B) between ecoregions in Madagascar and Australia. DES and TSMBF are in both Madagascar and Australia, and separated from non-shared ecoregions with a dotted line for clarity. Horizontal lines are used to emphasize the zero line. Significant differences between Madagascar and Australia (t-test) are indicated by asterisks: $p < 0.001$***, $p < 0.01$**, $p < 0.05$*. TBMF, temperate broadleaf and mixed forests; TGSS, temperate grasslands, savannahs, and shrublands; TSGSS, tropical and subtropical grasslands, savannahs, and shrublands; TSDBF, tropical and subtropical dry broadleaf forests; DES, deserts and xeric shrublands; TSMBF, tropical and subtropical moist broadleaf forests.

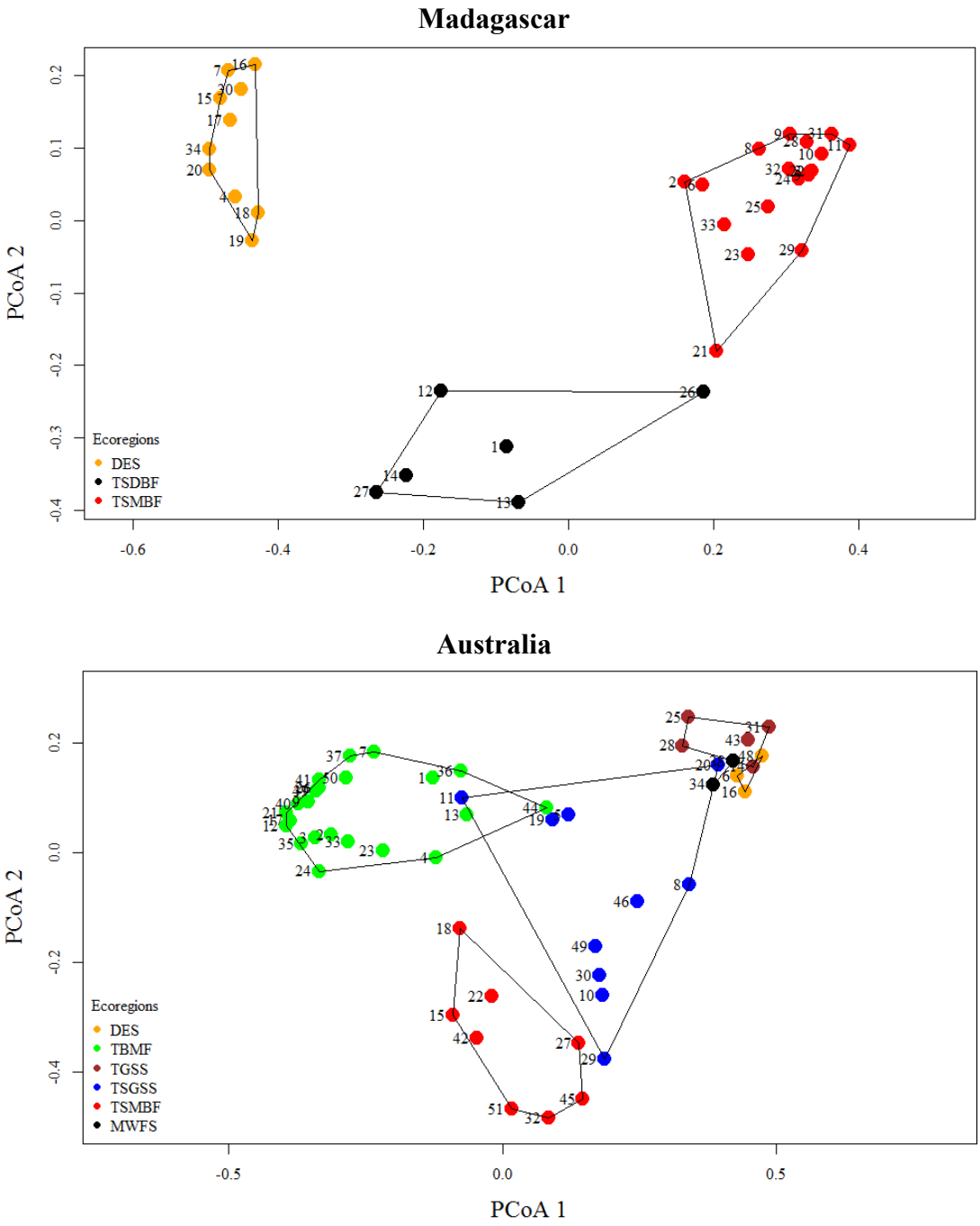


Figure 4.13. Principal Coordinate Analysis (PCoA) plot of the Jaccard index of compositional similarities by site for Madagascar and Australia's nonvolant mammal communities. Numbers indicate site numbers, shown in Table A.1 and A. 2. DES, deserts and xeric shrublands; MFWS, mediterranean forests, woodlands and scrub; TSDBF, tropical and subtropical dry broadleaf forests; TSMBF, tropical and subtropical moist broadleaf forests; TBMF, temperate broadleaf and mixed forests; TGSS, temperate grasslands, savannahs, and shrublands; TSGSS, tropical and subtropical grasslands, savannahs, and shrublands.

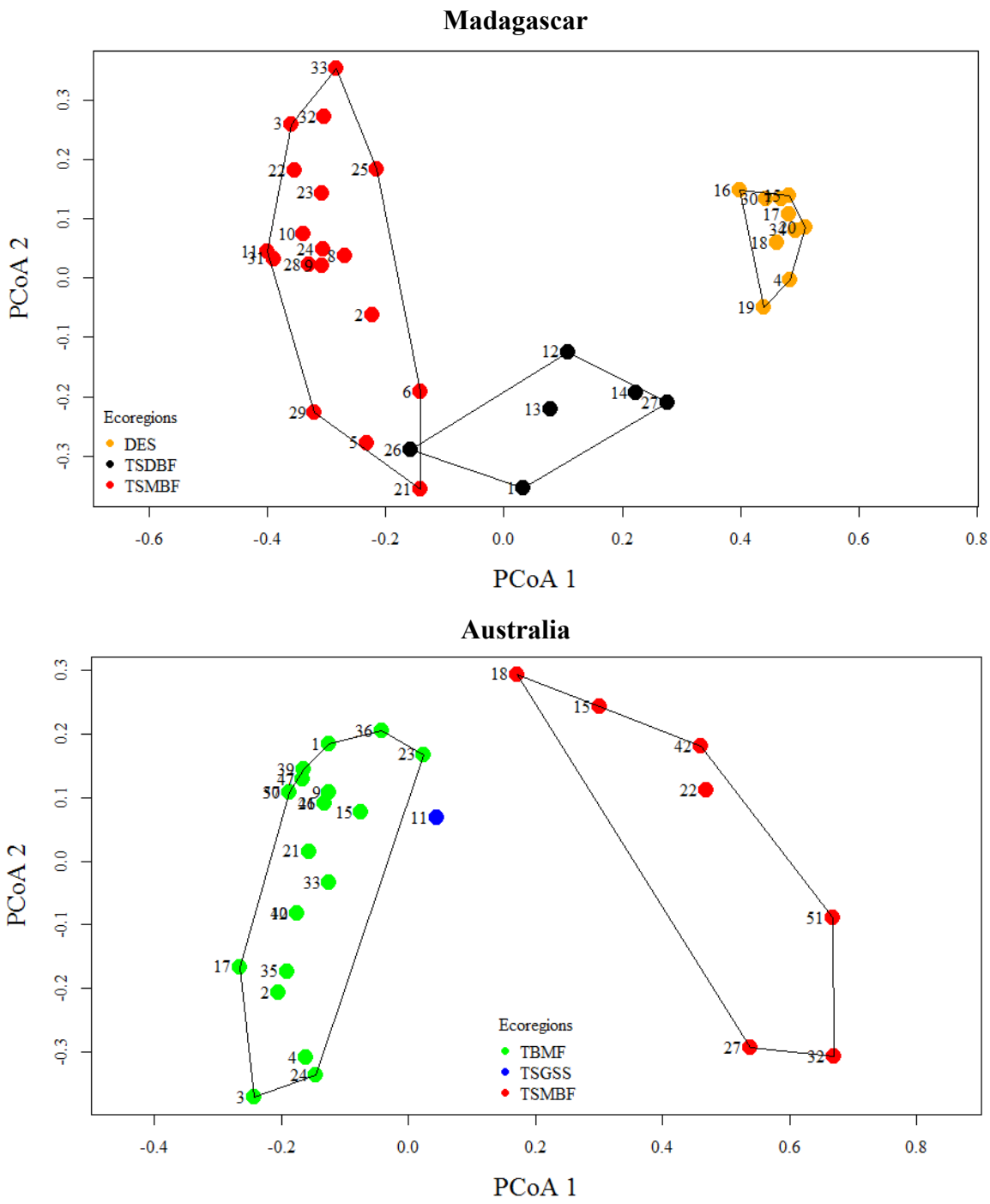


Figure 4.14. Principal Coordinate Analysis (PCoA) plot of the Jaccard index of compositional similarities by site for Madagascar and Australia's arboreal mammal communities. Numbers indicate site numbers, shown in Table A.1 and A. 2. DES, deserts and xeric shrublands; TSDBF, tropical and subtropical dry broadleaf forests; TSMBF, tropical and subtropical moist broadleaf forests; TBMF, temperate broadleaf and mixed forests; TSGSS, tropical and subtropical grasslands, savannahs, and shrublands.

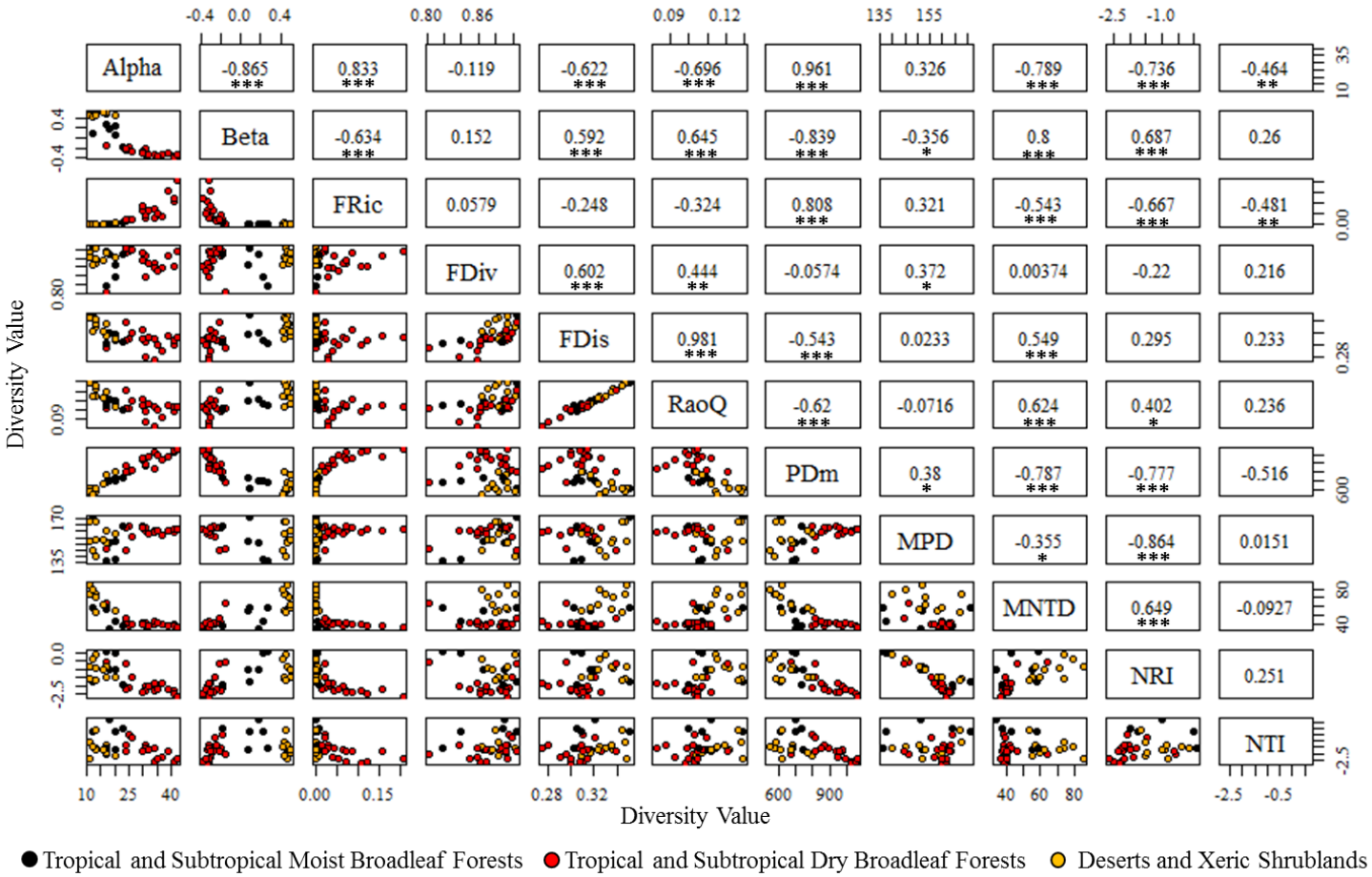


Figure 4.15.A. Correlation matrix of diversity measures for 34 nonvolant mammal communities in Madagascar. Points are coloured by ecoregion type. Pearson correlation coefficients (r) are provided in upper right of matrix. Significant correlations are denoted by asterisks: $p \leq 0.05$*, $p \leq 0.01$**, $p \leq 0.001$***. Abbreviations: FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index.

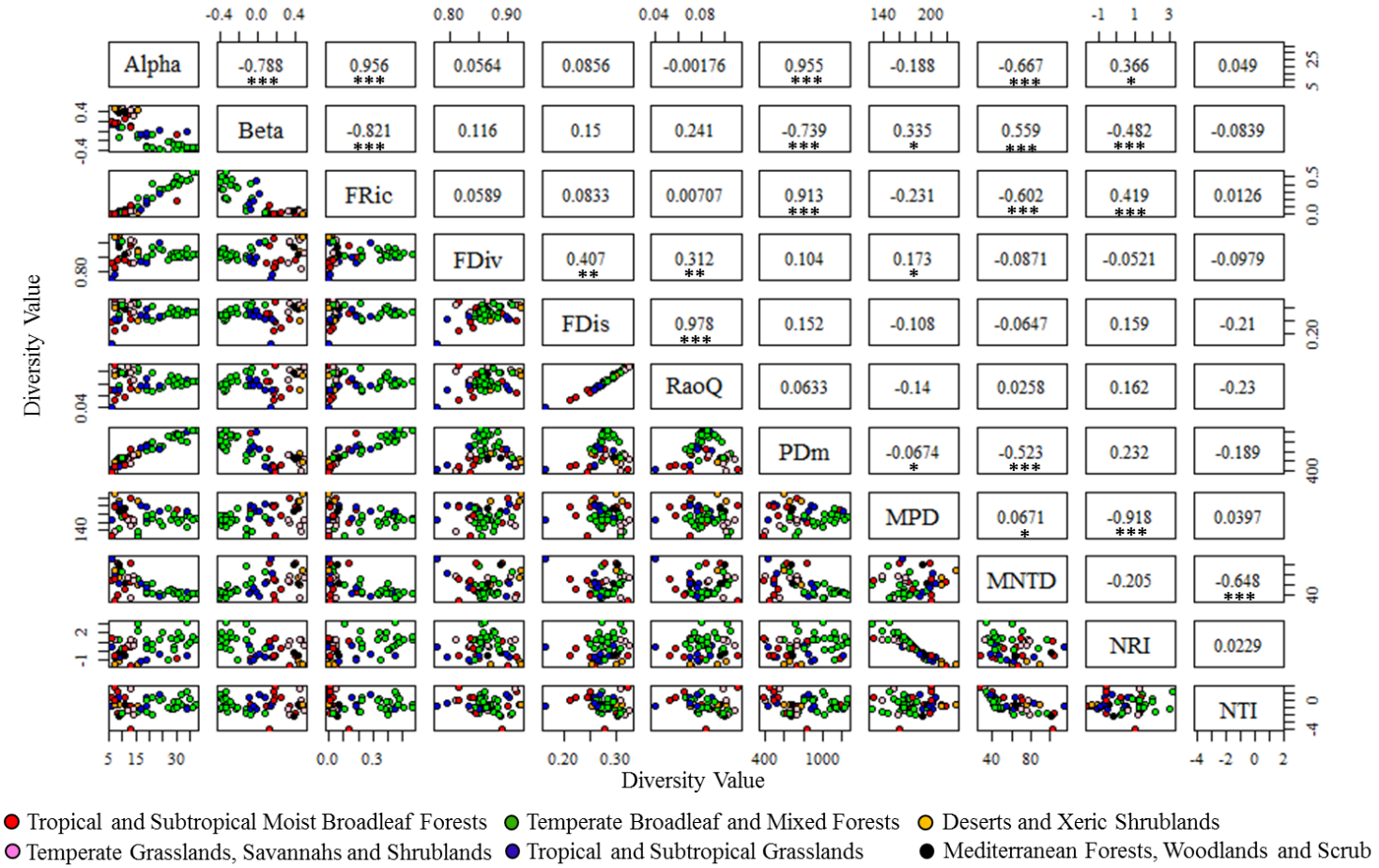


Figure 4.15.B. Correlation matrix of diversity measures for 51 nonvolant mammal communities in Australia. Points are coloured by ecoregion type. Pearson correlation coefficients (r) are provided in upper right of matrix. Significant correlations are denoted by asterisks: $p \leq 0.05$*, $p \leq 0.01$**, $p \leq 0.001$***. Abbreviations: FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index.

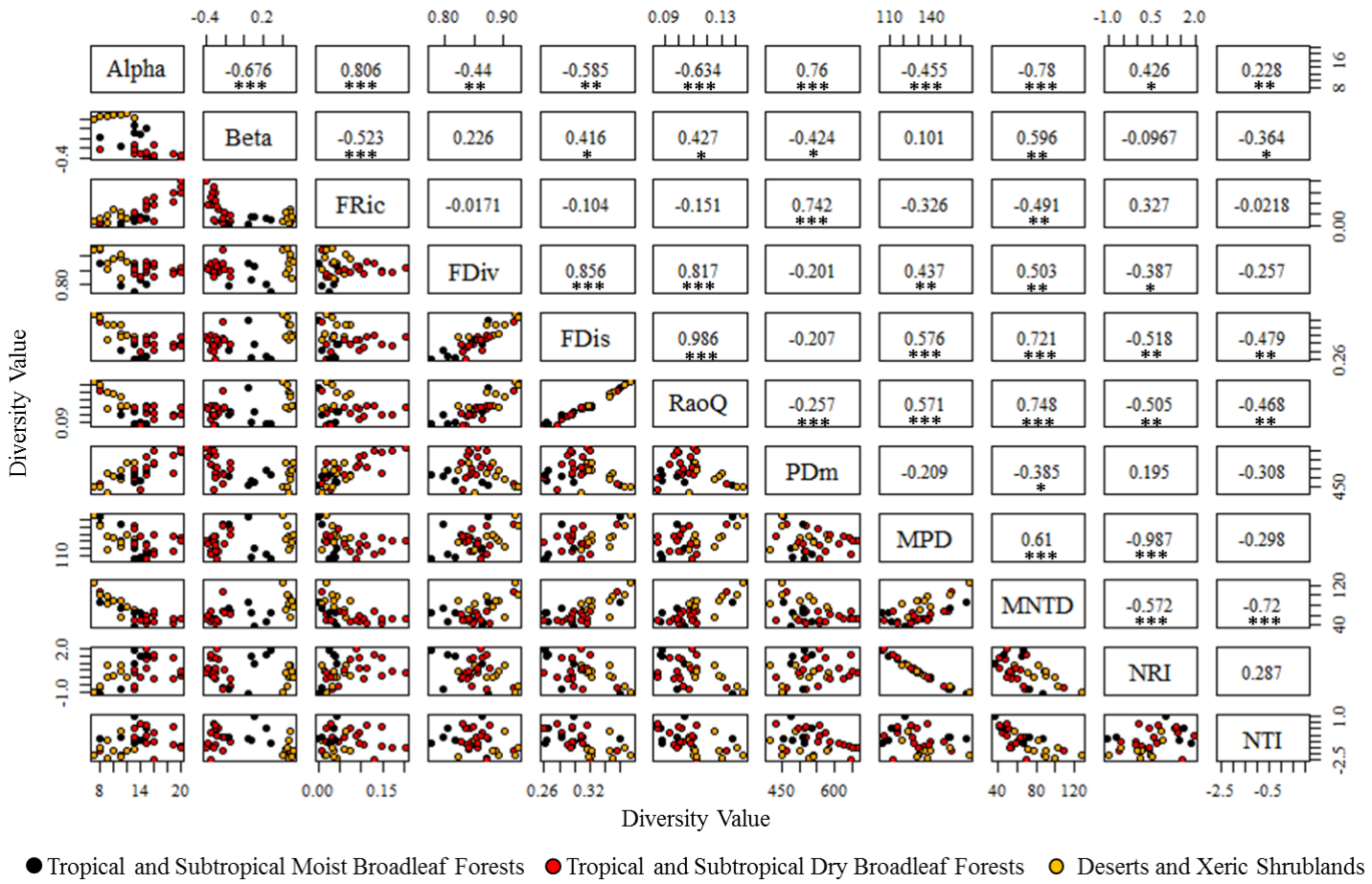


Figure 4.15.C. Correlation matrix of diversity measures for 34 arboreal mammal communities in Madagascar. Points are coloured by ecoregion type. Pearson correlation coefficients (r) are provided in upper right of matrix. Significant correlations are denoted by asterisks: $p \leq 0.05$*, $p \leq 0.01$**, $p \leq 0.001$***. Abbreviations: FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index.

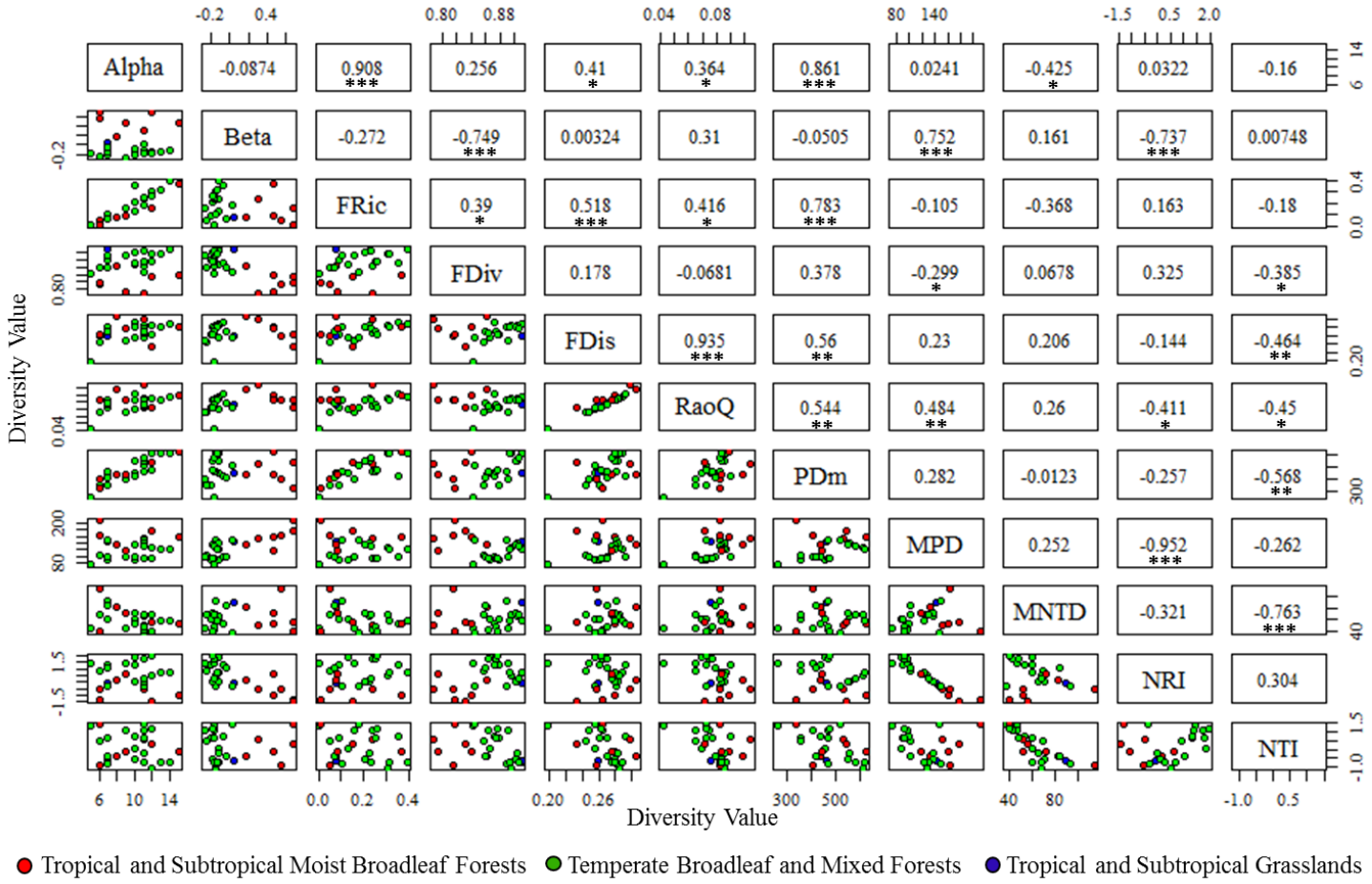


Figure 4.15.D. Correlation matrix of diversity measures for 30 arboreal mammal communities in Australia. Points are coloured by ecoregion type. Pearson correlation coefficients (r) are provided in upper right of matrix. Significant correlations are denoted by asterisks: $p \leq 0.05$*, $p \leq 0.01$**, $p \leq 0.001$***. Abbreviations: FRic, functional richness; FDiv, functional divergence; FDis, functional dispersion; RaoQ, Rao's quadratic entropy; PDm, phylogenetic diversity; MPD, mean pairwise distance; MNTD, mean nearest taxon distance; NRI, net relatedness index; NTI, nearest taxon index.

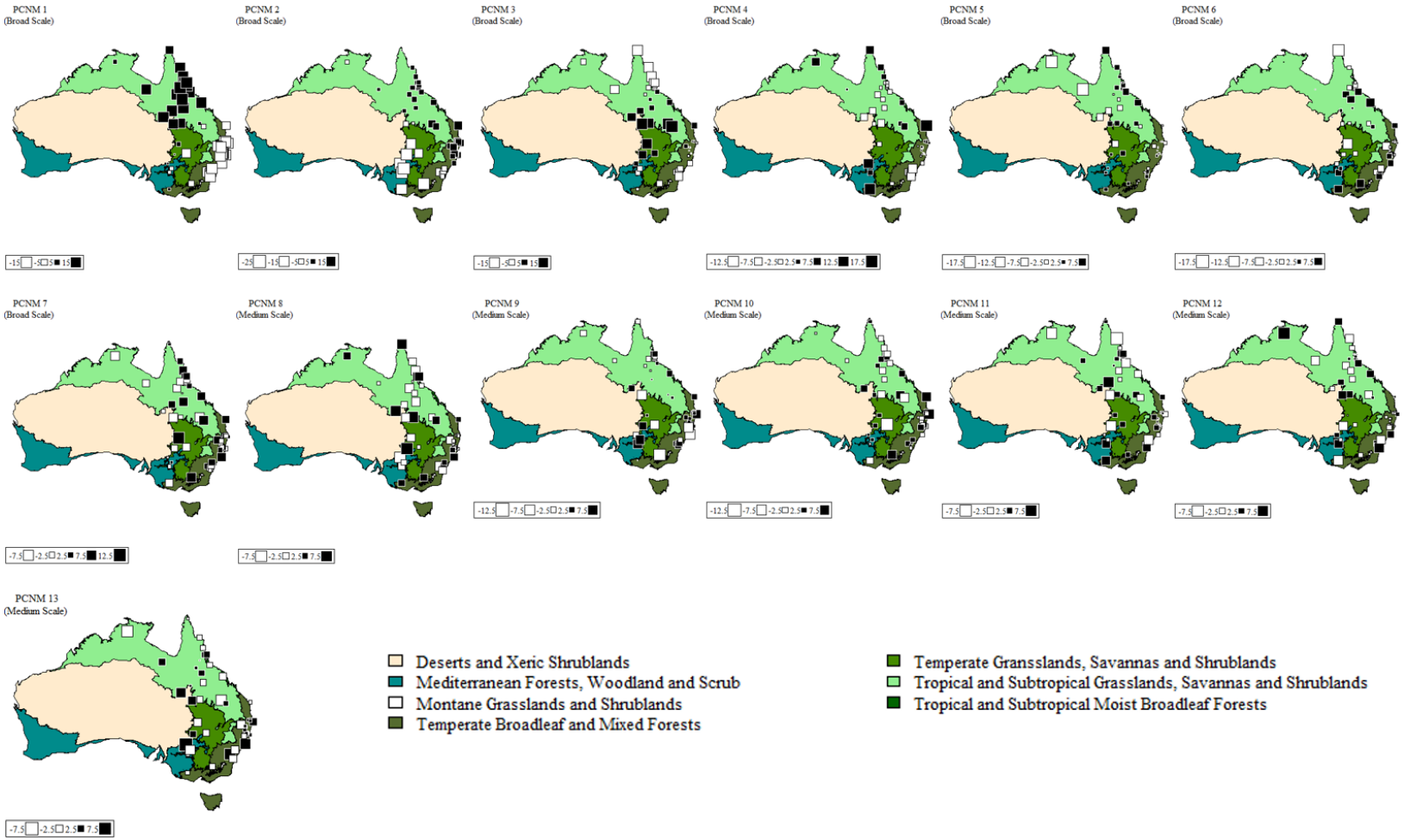


Figure 4.16. The significant forward selected Principal Coordinate of Neighbour Matrices (PCNM) variables in Australia with positive spatial correlation used in the PCNM analysis. PCNMs 1-7 depicted broad spatial scales and PCNMs 8-13 depicted medium spatial scales. The squares of similar size and colour represent sites with shared spatial scales. Filled squares: positive eigenvalues; empty squares: negative eigenvalues

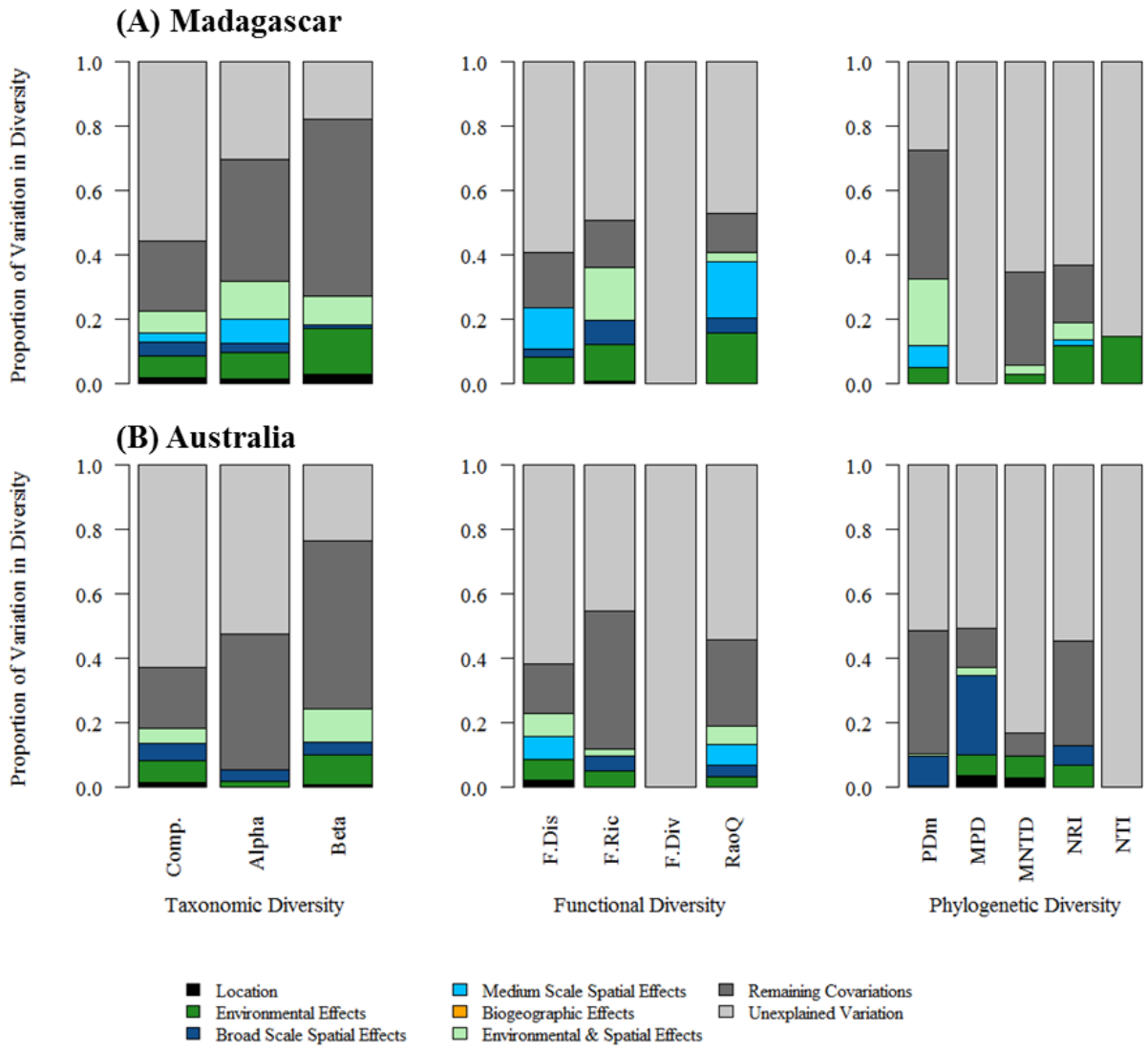


Figure 4.17. Percentage of variation due to location, environmental variables, spatial variables, and covariations for each measure of non-detrended diversity describing (A) Madagascar's and (B) Australia' nonvolant mammal communities.

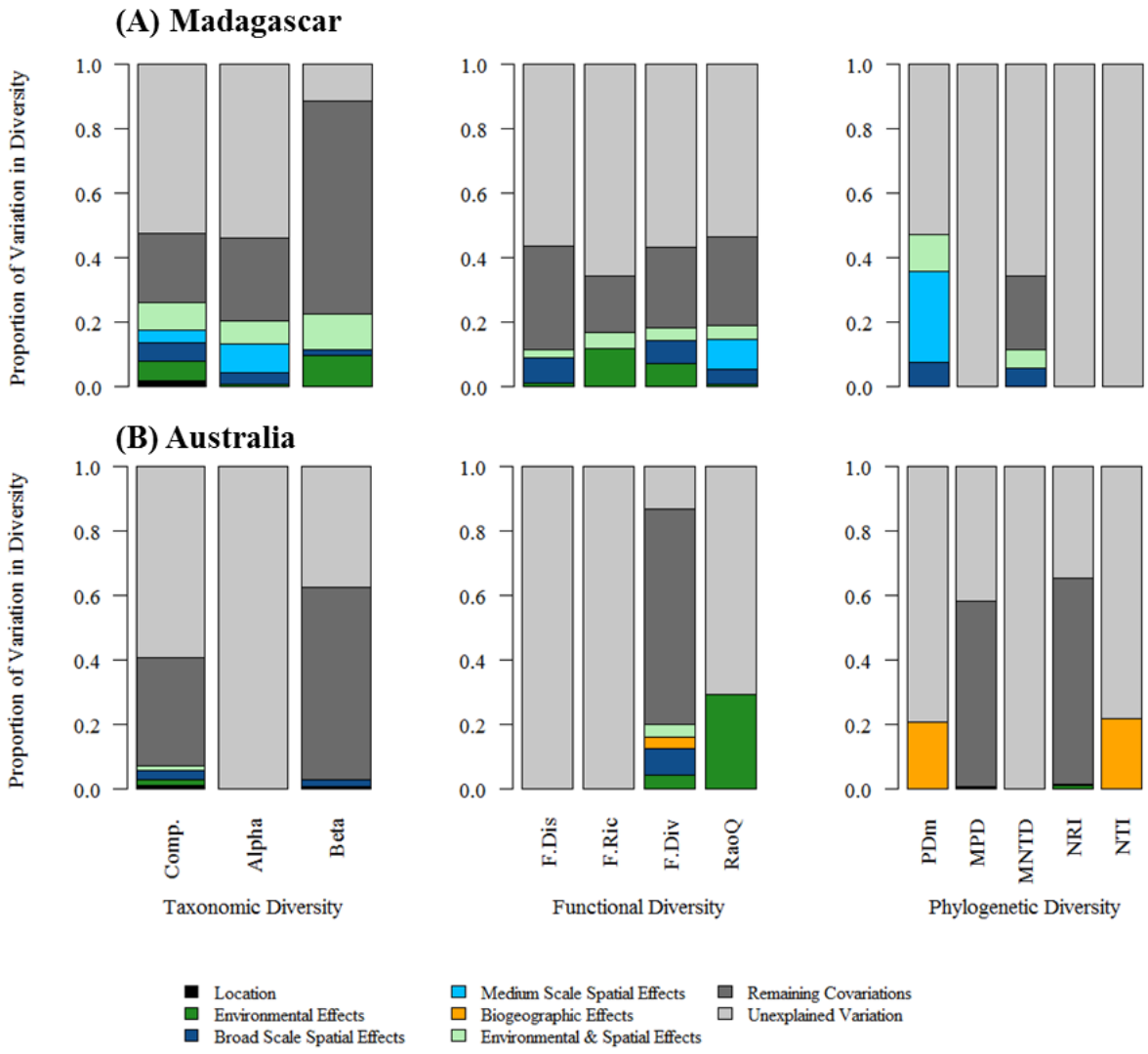


Figure 4.18. Percentage of variation due to location, environmental variables, spatial variables, and covariations for each measure of non-detrended diversity describing (A) Madagascar's and (B) Australia' arboreal mammal communities.

Chapter 5. Conclusions

This dissertation investigated the relative and combined roles of deterministic, stochastic and biogeographic assembly processes in shaping primate and nonvolant mammal communities to better understand extant patterns of community diversity. I described the nonvolant mammal communities in Madagascar and Australia using taxonomic, functional and phylogenetic diversity measures based on species occurrence data, eight traits related to resource use, and their molecular phylogenies. I used a unifying analytical approach to identify the assembly processes structuring community diversity at various spatial scales (Figure 1.6). Assembly processes were indicated with several environmental variables, spectral decomposition of the spatial relationships between sites, and a novel measure of site isolation by biogeographic barriers based on effective dispersal distances. This dissertation offers several important contributions to the study of community assembly particularly for primate and mammal diversity in Madagascar, including (1) identification of the unique and combined components of variation in diversity that are attributable to deterministic, stochastic and biogeographic assembly processes, (2) an investigation of multiple types of diversity (taxonomic, functional, and phylogenetic), and (3) a scale explicit comparative approach, that highlights the regional specificity of assembly processes and the potential limitations of large macroscale models.

CONTRIBUTIONS AND CHAPTER OVERVIEW

Four guiding questions for the dissertation were presented in the introduction, which this dissertation was able to address.

(1) Are arboreal and terrestrial species separately shaped by dispersal limitation and environmental sorting?

In Chapter 2, I provided an analysis of the assembly processes shaping Madagascar's nonvolant mammal community composition using spectral decomposition of the spatial relationships among 34 study sites and variation decomposition to describe and compare primates to non-primate mammals, and arboreal mammals to terrestrial mammals to detect varying patterns of community assembly in Madagascar. I also introduced a novel measure for including the contribution of biogeographic dispersal barriers to site isolation. This measure was based on the effective distance of travelling over or around biogeographic barriers. I found that environmental and spatial effects, indicating the operation of environmental sorting and dispersal limitation, almost equally explained compositional patterns of nonvolant mammal communities. Arboreal and terrestrial mammal communities were separately shaped by dispersal limitation and environmental sorting. Dispersal limitation by distance provided a better explanation for compositional variation in primate and arboreal mammal communities, especially at broad spatial scales, than environmental sorting. By contrast, only environmental sorting explained non-primate and terrestrial mammal distributions. Biogeographic effects were not significant for any community type.

Although the majority of theoretical developments in the field of community assembly have been on non-motile taxa, the study of motile taxa has suggested that dispersal limitation is more important for arboreal species than terrestrial species (e.g.,

Lindo and Winchester 2009, chapter 2). In addition to limited dispersal between forested areas, the matrix between arboreal habitats and the functional flexibility of arboreal species being able to survive or travel through the matrix are also influencing factors that require more consideration. Furthermore, functional adaptations to arboreal environments may also correlate with high dietary specificity that makes surviving outside of arboreal environments difficult. The inclusion of additional environmental variables (e.g., dispersal species-level surfaces) and trait data (e.g., dispersal distance, frequency) in future studies will help separate the stochastic process of dispersal limitation by distance between arboreal communities and the deterministic functional differences (cf. Lowe and McPeek 2014), or environmental features that are influencing patterns of arboreal mammal diversity. Finally, the matrix between protected areas can be the result of anthropogenic disturbance (e.g., Prugh et al. 2008), which would be useful to examine as a separate influencing factor shaping patterns of extant diversity.

(2) Do deterministic, stochastic, and biogeographic processes differentially explain taxonomic, functional, and phylogenetic diversity measures of community richness?

Taxonomic (taxonomic identity of species), functional (the functional role species are playing in an ecosystem) and phylogenetic diversity (amount of evolutionary history each species contributes) patterns often differ (Pavoine and Bonsall 2011; Figure 1.3), generating various community assembly interpretations (e.g., Kraft and Ackerly 2010; Meynard et al. 2011; Pavoine and Bonsall 2011). Furthermore, functional differences can shape the relative importance of assembly processes (chapter 2). Consequently, in chapter 3 and 4 I provided an investigation of how different measurement indices of taxonomic, functional and phylogenetic diversity affect the detection of different community assembly processes.

In chapter 3, I quantified taxonomic, functional and phylogenetic diversity patterns in Malagasy primate communities in eastern and western Madagascar and across ecoregions. Latitude- (east versus west) and ecoregion- specific patterns in diversity were found for taxonomic, functional and phylogenetic diversity. Eastern Madagascar and the humid ecoregions had higher species richness and lower functional diversity values. Eastern communities were also characterized by older species and distantly related co-occurring species. Biogeographic dispersal barriers leading to site isolation explained only a minor proportion of variation in composition. Environmental sorting and dispersal limitation by distance were found to shape both the taxonomic diversity and the functional diversity of primate communities in Madagascar. Phylogenetic diversity was poorly explained by the variables tested, and both environmental sorting and dispersal limitation by distance explained different phylogenetic diversity metrics. For all three diversity types covariations between location, environmental variables and spatial variables explained large proportions of variation in diversity measures, highlighting intrinsic relationships between variables related to ecoregional variations within Madagascar. Ecoregional differences strongly contributed to the observed patterns of environmental sorting and dispersal limitation with clear bioclimatic differences present in Madagascar. Madagascar's primate communities are the result of widespread diversification into novel habitats and the combined action of deterministic and stochastic assembly processes shaping the taxonomic and functional diversity of communities. In chapter 4, I extended this multi-diversity approach to the study of nonvolant and arboreal mammal communities in Madagascar and Australia. Taxonomic mammal diversity in both Madagascar and Australia was shaped by the combined action of variables depicting environmental sorting and dispersal limitation by distance. In addition, spatial-environmental covariation explained large components of variation in most diversity

measures that could be modeled. Phylogenetic diversity across groups was variably explained by environmental sorting, dispersal limitation by distance and biogeographic barriers.

In answer to this second question, different types of diversity are in some respect variably assembled. Taxonomic, functional, and phylogenetic measures of diversity were not explained in equal proportions by the same set of variables. Taxonomic and functional diversity measures had more variation explained by the suite of variables used in this dissertation than phylogenetic measures of diversity. Phylogenetic measures provided weak indicators of assembly overall. This result could be because phylogenetic diversity was randomly structured with a tendency to overdispersion in both Madagascar and Australia, making identifying patterns in its distribution difficult. Or the difference could be because phylogenetic measures do not provide clear mechanistic explanations for assembly scenarios, and require knowledge of the relationship between functional and phylogenetic diversity to appropriately interpret assembly.

Different measures of diversity (i.e. taxonomic, functional, and phylogenetic) describe different facets of diversity and their potential responses to environmental and spatial attributions of their habitats (Meynard et al. 2011; Münkemüller et al. 2012; Pavoine and Bonsall 2011; Stegen and Hurlbert 2011; Swenson 2011). Assembly of taxonomic diversity, at least to the species or subspecies level, describes the current state of species diversification and how species in their current distributional patterns are shaped. Functional diversity ignores species identity and instead measures how traits are dispersed in space or along environmental gradients, identifying if traits are functional adaptations to specific environmental features or competitive regimes. Finally, phylogenetic diversity encapsulates the genetic and phenotypical history of differentiation and the temporal scale separating species, providing a ‘deeper’ temporal metric of

differentiation between communities. Because of these critical differences between diversity components, their differential explanation by explanatory variables is not surprising and is expected.

(3) Can patterns in process be generalized across ecoregions, and do they show patterns of convergence across regions of similar biogeographic and evolutionary histories?

Previous studies have suggested that Madagascar is globally unique in its evolutionary history (Vences et al. 2009), climate (Dewar and Richard 2007), endemic fauna, mammalian trait distributions (Dewar and Richard 2007; Wright 1999), and more recently the assembly patterns explaining primate community diversity (Beaudrot and Marshall 2010). However, previous comparisons of primate communities have been to geographic regions with disparate biogeographic and evolutionary histories from Madagascar. Consequently, Madagascar appears as an outlier. A more appropriate comparison of Madagascar's mammal communities may be to Australia, a region that is also bounded in space, has been isolated for millions of years, has high faunal endemicity, and the presence of arboreal mammal communities that show functional divergence to Malagasy lemurs (Smith and Ganzhorn 1996). Furthermore, Australia and Madagascar share structurally and floristically similar habitats in the tropical and subtropical moist broadleaf forests and the deserts and xeric shrublands ecoregions, and unique habitat types present in their nonshared ecoregions (Olson et al. 2001; Smith and Ganzhorn 1996). Chapter 4 consequently provided a test of convergent assembly scenarios in nonvolant and arboreal mammal communities from Madagascar and Australia. Patterns in nonvolant mammal diversity and community assembly in Madagascar and Australia were inter- and intra-regionally variable. Despite similar

biogeographic histories, patterns of insular mammal evolution, shared ecoregions, and convergent niches in Australian possums and Malagasy lemurs, support for convergent diversity and assembly patterns only existed for nonvolant mammals. Arboreal mammals had convergent functional richness values but did not share patterns of assembly. This analysis calls into question the search for overarching explanations for patterns of diversity or assembly when significant environmental heterogeneity and variations in diversity characterize mammal communities. Broad-scale regional descriptions of community assembly patterns may be unrealistic even for regions with comparable histories. Overall, patterns of mammal diversity in Madagascar and Australia were the result of environmental sorting, dispersal limitation, and evolutionary processes. This study provided further evidence that assembly processes do not operate in isolation but instead work in concert to shape patterns of community diversity.

The detection of community assembly processes requires spatially explicit approaches because ecological interactions and variables describing environmental, biogeographic, and spatial attributes are spatially scaled. Ecoregional descriptions, or environmental regions that share climatic and floristic structures, are in part spatially structured. Consequently, patterns of diversity and assembly processes are to some degree ecoregionally unique based on the scale of inquiry and describe enough intra-regional complexity that patterns are not convergent across ecoregions, even when measures that do not use species identities are used, e.g., functional diversity. Ecoregional classifications have been a popular tool for setting conservation priorities, describing patterns of biodiversity distributions, and discussing evolutionary changes over time (e.g., Cardillo 2011; Fritz et al. 2009; He and Zhang 2009; Thompson et al. 2005). There is merit to classifying major habitat types within large regions, such as within Madagascar and Australia, by the broad-scale climatic and floristic structures they describe. However,

comparing such major habitat type classifications between regions is complicated by the contribution of the specific biogeographic and evolutionary histories that have occurred in each region. Although convergent functional patterns may exist in a few taxa (e.g., Smith and Ganzhorn 1996), they may not result in convergent patterns at the community-level, as shown in chapter 4. Large macro-scale studies of community assembly processes may be inappropriate for understanding patterns of species distributions when the biogeographic and evolutionary histories are superficially similar but are temporally and spatially unique and have resulted in a complex array of fauna that have been assembly in regionally unique ways (cf. Pavoine and Bonsall 2011).

Madagascar is often discussed as a unique 'island continent' with high levels of species endemicity, and characterized by mammal populations with unique suites of traits that are the result of a long period of isolated evolution (Ganzhorn et al. 2014; Wright 1999). However, previous comparisons of Madagascar to other biogeographic areas were comparisons to large-scale continental land-locked bodies with varied evolutionary histories (e.g., Beaudrot and Marshall 2011; Reed and Bidner 2004; Wright 1999), which often resulted in Madagascar not fitting global models and appearing as an outlier, and has contributed to its recognition as an area of conservation priority and uniqueness. While, I do not discount its uniqueness as illustrated by its large endemic population, I did want to see how it would compare to an area with more similarities in biogeographic and evolutionary histories of its endemic fauna than differences, which Australia provided (cf. Smith and Ganzhorn 1996). However, patterns of diversity were regionally and ecoregionally unique. While Madagascar and Australia may provide better comparisons for each other than Madagascar to continental Africa, their respective nonvolant populations are regionally and ecoregionally unique and are not explained by the same suites of assembly processes. Instead, ongoing anthropogenic modification, the

impact of nonindigenous competitors and ecogeographic variation that characterizes the ecoregions of Madagascar and Australia have resulted in diverse mammal communities that are regionally-specific and the result of both environmental sorting and dispersal limitation.

DIVERSITY AND COMMUNITY ASSEMBLY

Functional Diversity

Functional diversity is a rapidly growing area of ecological research, with several new metrics proposed in the last decade (Laliberté and Legendre 2010; Mason et al. 2005; Mouchet et al. 2010; Petchey and Gaston 2006; Schleuter et al. 2010). Functional diversity measures are trait dependent and have a variety of caveats regarding their use. Some measures require abundance data, no missing data, and cannot have more traits than species in a community (Laliberté and Legendre 2010; Mouchet et al. 2010). The relationship between functional diversity metrics and assembly processes are not always clear, continued research is required to develop clear relationships between functional diversity metrics and assembly processes (Mouchet et al. 2010; Pavoine and Bonsall 2011). Consequently, I encourage the continued use of functional diversity in biological anthropology, and the inclusion of trait types that uniquely identify groups of species, such as social traits or traits describing ecological interactions in primates and mammals.

Trait selection allows for tests of explicit hypotheses on the relationship between trait structures and assembly processes. Simulation of communities have shown that niche-based processes (environmental sorting and competition) dominate for communities of large populations sizes and homogeneous environments and that neutral processes (dispersal limitation) dominate for species with small populations sizes and heterogeneous environments (Fisher and Mehta 2014). This dissertation showed that

functional differences in dispersal (i.e. terrestrial versus arboreal species) can also result in differences between niche-based and neutral-based processes shaping community composition and diversity (chapters 2 and 4; also Lindo and Winchester 2009). Additional trait data are required to investigate the influence of additional dispersal related traits, including dispersal distances, migratory patterns, and dispersal behavior to distinguish between stochastic and deterministic dispersal differences shaping community assembly (cf. Lowe and McPeek 2014). In addition, more mammal- and site- specific studies of inter-specific interactions at the local scale are needed to parse out the relative contributions of competition and environmental sorting to patterns of assembly in mammal communities.

Phylogenetic Diversity

The use of phylogenetic diversity measures for the study of community assembly is compromised by the lack of clear mechanistic hypotheses describing how patterns of phylogenetic overdispersion and clustering demonstrate the action of environmental sorting or competition because both patterns can be due to either assembly process (Kembel 2009; Pavoine and Bonsall 2011; Warren et al. 2014). A detailed understanding of past evolutionary transitions, patterns of speciation and the role of biogeography leading to extant patterns of phylogenetic distributions are required to identify the predominant community assembly processes shaping observed patterns of phylogenetic diversity. The study of phylogenetic diversity at various spatial scales has been used to identify the relative roles of environmental filtering and competition (Warren et al. 2014). For example, environmental sorting and speciation are separately investigated at local and broad regional spatial scales because competitive interactions are expected to be more important at small spatial scales in contrast to broad scales that can reveal the

contribution of macroevolutionary and biogeographic processes, including speciation and range shifts (reviewed in Warren et al. 2014). However, without explicitly considering the operation of each set of processes (environmental sorting, competition, speciation, biogeographic barriers) erroneous conclusions regarding the most important assembly process exist (Warren et al. 2014). Consequently, contributions such as the effective distance ratio introduced in this dissertation to depict the contribution of biogeographic dispersal barriers to patterns of assembly, can help better identify the contribution of biogeographic barriers to observed diversity patterns.

Assumptions

A commonly held assumption in the study of biodiversity, is that closely related species are functionally related (Darwin 1859). However, for nonvolant mammals in Madagascar and Australia, this pervasive assumption did not hold at the community level. A caveat to this result, however, is that the traits used in this analysis may not be phylogenetically conserved, while other traits might provide a different result (e.g., Kamilar and Cooper 2013). For example, body mass is strongly phylogenetically conserved in primates (Kamilar et al. 2012; Kamilar and Cooper 2013), while climatic niches are not (Kamilar and Cooper 2013; Kamilar and Muldoon 2010). Old World primates have phylogenetically conserved social systems (Di Fiore and Rendall 1994), and gestation length, litter size and territoriality are conserved in primates generally (Kamilar and Cooper 2013). However, this dissertation was concerned with investigating traits that are related to resource use and species ecological interactions, consequently traits were carefully chosen to reflect axes of resource use that were collectible for a large number of mammal species. Furthermore, limited *a priori* expectations of highly correlated phylogenetic and functional diversity exist for species that are the result of

extensive and rapid adaptive radiations, including the mammals of Madagascar and Australia. Consequently, the lack of a strong correlation between functional diversity and phylogenetic diversity for the mammals of Madagascar and Australia identified in this dissertation is not surprising. In light of the critiques associated with the utility of phylogenetic diversity measures for the study of assembly, more research is needed: (1) to create variables, such as the biogeographic effective distance ratio introduced here, to identify historic and biogeographic influences on extant patterns of phylogenetic diversity, (2) to investigate temporal assembly patterns, and (3) to develop phylogenetic diversity metrics that better parse out competing assembly hypotheses. I caution against the uncritical use of phylogenetic diversity measures as a silver bullet approach to studying assembly of diversity in any fauna, without first testing its relationship to trait distributions.

FUTURE DIRECTIONS

Implications for the Study of Evolution

Stochastic, deterministic and biogeographic processes have all been studied as separate forces shaping primate and hominin evolution, but not as integrated models. Rich paleoecological datasets, including both community composition and environmental attributes, exist for important primate and human fossil sites (e.g., Reed 2008; Su and Harrison 2008) that can provide the interpretive framework for asking and answering questions related to human and primate evolution from a community perspective. The community perspective in studies of evolution provides a framework for investigating the range of ecological and environmental pressures that may have shaped evolutionary trajectories, and identifying the processes that shape such communities is a step in that direction. Furthermore, the fossil record allows for the examination of the potential

effects of interaction among co-occurring species over long time periods and large spatial scales (Jablonski and Sepkoski 1996). The methods employed in this dissertation are applicable to small sample sizes, missing data, and occurrence data that predominates in fossil data (e.g., Barnosky et al. 2005; Svenning et al. 2011). Furthermore, this dissertation has highlighted the utility of investigating various aspects of diversity that are detectable with fossil materials. Functional diversity, in particular, provides a crucial new suite of metrics that allows for detailed trait data collected from fossil materials to serve as a measure of diversity without committing circular taxonomic or phylogenetic diversity assignments that are based on extant fauna and the assumption that phylogenetically related species are also functionally related.

Simultaneous tests of the roles of deterministic, stochastic, and biogeographic processes in shaping ecological communities within which humans and primates evolved have the ability to greatly improve reconstructions of the ecological pressures that shaped communities and both primate and hominin evolution. Such a research approach may be able to explain the absence of species or fossils in areas that they appear to be ecologically adapted (because of biogeographic barriers or dispersal limitation), and provides anthropologists with tools for explaining variation in extinct communities that cannot be explained by deterministic hypotheses alone (e.g., Belyea 2007). Additionally, the study of temporal changes in community assembly over evolutionary time can help identify where additional processes are operating. For example, priority effects are a stochastic assembly process where the order of arrivals dictates success and helps shape community diversity (Chase 2010; Connell and Slatyer 1977; Ejrnæs et al. 2006; Leibold et al. 2004; Shulman et al. 1983; Sutherland 1974). Mergeay et al (2011) investigated the contribution of priority effects over long paleo-temporal scales in zooplankton (*Daphnia* spp.), finding that priority effects and environmental sorting had varying roles based on

habitat characteristics and the period investigated. Investigating the contribution of priority effects over time and the dispersal and speciation history of mammal communities over evolutionary time is the critical next step in understanding extant patterns of community assembly and diversity distributions.

Implications for Conservation

Predicting how communities respond to anthropogenic disturbance or climate change is a fundamental aim of conservation research, and environmental perturbations do affect the assembly patterns that shape ecological communities (Gilman et al. 2010; Lasky and Keitt 2013; Van der Putten et al. 2010). Analysis of the varied influences of ecological processes, such as disturbance, on patterns of biodiversity at different spatial scales is critical (Holt 2006, Chase 2007) for developing policies on community-level conservation, including habitat preservation and climate change. Mammal community composition can differ significantly between environmentally variable microhabitats and areas of disturbance, and never converge on similar species composition (e.g., Lomolino and Perault 2000). Assembly differences between communities also have implications for conservation. For example, the species or trait composition of a community that is more strongly deterministically-structured is more stable than that of a stochastically-structured community in a static environment (Purves and Turnbull 2010). In addition, a deterministic community shows more pronounced and predictable directional responses to environmental change (Purves and Turnbull 2010). With nearly half of the 634 primate species in the world classified as threatened or endangered on the IUCN Red List (Mittermeier et al. 2009), accurate predictive models are in great demand but can only be developed with a comprehensive understanding of the processes that shape mammal community composition. Furthermore, if the relative role of each ecological process

varies by spatial scale (e.g., Cadotte 2007, this dissertation), then local, national, and global conservation management plans can be better formulated once scale-specific processes and factors shaping extant communities are understood.

Continued research on the impacts of anthropogenic disturbance and climate change on primate and mammal diversity in Madagascar require further investigation. Simulation studies investigating the contributing effects of fragmentation on tree community assembly and ideal reserve sizes have suggested that reserve size variation and species diversity tradeoffs exist, where different reserve sizes preserve different types of diversity (Lasky and Keitt 2013). For example, species richness and dispersal limitation are increased in large protected areas, whereas gamma richness, plant productivity and environmental sorting are higher in small protected areas (Lasky and Keitt 2013). Source-sink dynamics and their influence on the diversity type of interest need to be identified to appropriately consider the impact of mass effects (Gravel et al. 2006; Leibold et al. 2004; Mouquet and Loreau 2003), environmental sorting and dispersal limitation on the maintenance of diversity (Lasky and Keitt 2013), and these impacts need to evaluated for mammal populations. This dissertation has shown that large-scale modeling of species distributions that rely on deterministic processes (such as niche-based species distribution models, e.g., Lozier et al. 2009; Thorn et al. 2009) should also consider dispersal limitation and biogeographic processes because environmental sorting does not operate in isolation. In addition, functional differences in diversity can be the result of different assembly processes or unmeasured variables that need to be considered and incorporated into predictive models or conservation plans (e.g., chapter 2). Finally, a scale-sensitive understanding of process and biodiversity distributions can aid scenario-based projections of species' distribution shifts in response to climate change and land-use changes (Jetz et al. 2007; Settele et al. 2008; Thuiller et

al. 2005). This dissertation demonstrates the use of methods that are useful for identifying which factors are relevant to community composition and diversity at particular spatial scales, which are required for informing the conservation of biodiversity across all spatial scales (Keil et al. 2012).

CONCLUSIONS

Community assembly patterns are not ubiquitous across diversity measures, mammal groups, or regions, nor do they operate in a mutually exclusive manner. Mammal communities in Madagascar and Australia are regionally unique, with strong ecoregional and latitudinal structuring due to bioclimatic differences across the island and the contribution of environmental sorting and dispersal limitation to the assembly of taxonomic and functional diversity patterns. My dissertation demonstrated that assembly processes do not operate in isolation, and an integrated multi-diversity approach to understanding mammal community patterns provides important insights regarding the interaction of multiple processes on the taxonomic, functional and phylogenetic structure of ecological communities. Further research is needed to identify how different components of diversity (taxonomic, phylogenetic, and functional) interact to provide accurate and informative interpretations of community assembly scenarios. The combined investigation of phylogenetic and functional diversity and biogeographic variables provide a crucial set of tools for parsing the contribution of assembly processes over spatial and temporal scales. With methodological advances that now allow for the study of assembly on multiple types of diversity and occurrence data, studies of community assembly in paleocommunities are possible.

Appendix: Nonvolant mammal data included in analyses

Table A.1. Malagasy occurrence lists per site for all nonvolant mammal species included in analyses. Publication cut-off date for included sources of information was January 2012.[a]

Site ID#	Site	Species Occurrence [b]
1	Ambohijanhary	*Cheirogaleus crossleyi, Cryptoprocta ferox, Eliurus majori, Eliurus myoxinus, Eulemur rufus, Eupleres goudotii, Galidia elegans, Microgale longicaudata, Microgale majori, Propithecus deckenii, Setifer setosus, Tenrec ecaudatus*
2	Ambohitantely	*Avahi laniger, Cryptoprocta ferox, Eliurus minor, Eulemur fulvus, Hapalemur griseus, Microcebus rufus, Microgale cowani, Microgale dobsoni, Microgale gymnorhyncha, Microgale longicaudata, Microgale majori, Microgale parvula, Microgale pusilla, Microgale talazaci, Oryzorictes hova, Setifer setosus, Tenrec ecaudatus*
3	Analamazaotra	*Allocebus trichotis, Avahi laniger, Brachytarsomys albicauda, Cheirogaleus crossleyi, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus minor, Eliurus tanala, Eliurus webbi, Eulemur fulvus, Eulemur rubriventer, Eupleres goudotii, Fossa fossana, Galidia elegans, Gymnuromys roberti, Hapalemur griseus, Hemicentetes semispinosus, Indri indri, Lepilemur mustelinus, Microcebus lehilahytsara, Microgale cowani, Microgale drouhardi, Microgale gracilis, Microgale pusilla, Microgale taiva, Microgale talazaci, Microgale thomasi, Nesomys audeberti, Nesomys rufus, Oryzorictes hova, Propithecus diadema, Setifer setosus, Tenrec ecaudatus, Varecia varecia*
4	Analavelona	*Cheirogaleus medius, Cryptoprocta ferox, Echinops telfairi, Eliurus myoxinus, Eulemur rufus, Lemur catta, Lepilemur ruficaudatus, Microcebus murinus, Microgale majori, Microgale nasoloi, Phaner pallescens, Propithecus verreauxi, Tenrec ecaudatus*
5	Andohahela Parcel 1 – Humid [c]	*Avahi meridionalis, Cheirogaleus major, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus majori, Eliurus minor, Eliurus tanala, Eliurus webbi, Eulemur collaris, Eupleres goudotii, Fossa fossana, Galidia elegans, Galidictis fasciata, Gymnuromys roberti, Hapalemur meridionalis, Microcebus rufus, Microgale cowani, Microgale dobsoni, Microgale fotsifotsy, Microgale gracilis, Microgale longicaudata, Microgale majori, Microgale parvula, Microgale principula, Microgale soricoides, Microgale taiva, Microgale talazaci, Microgale thomasi,*

Site ID#	Site	Species Occurrence [b]
		Nesomys rufus, Oryzorictes hova, Tenrec ecaudatus
6	Andohahela Parcel 1 – Subhumid [c]	*Avahi meridionalis, Cheirogaleus major, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus majori, Eliurus minor, Eliurus tanala, Eliurus webbi, Eulemur collaris, Fossa fossana, Galidia elegans, Galidictis fasciata, Gymnuromys roberti, Hapalemur meridionalis, Lepilemur fleuretae, Microcebus rufus, Microgale dobsoni, Microgale fotsifotsy, Microgale longicaudata, Microgale parvula, Microgale principula, Microgale thomasi, Propithecus verreauxi, Setifer setosus, Tenrec ecaudatus*
7	Andohahela Parcel 2	*Cheirogaleus medius, Cryptoprocta ferox, Echinops telfairi, Eliurus myoxinus, Geogale aurita, Lemur catta, Lepilemur leucopus, Microcebus griseorufus, Phaner pallescens, Propithecus verreauxi, Tenrec ecaudatus*
8	Andringitra – Humid [c]	*Avahi laniger, Cheirogaleus major, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus minor, Eliurus tanala, Eliurus webbi, Eulemur cinereiceps, Eulemur fulvus, Eulemur rubriventer, Fossa fossana, Galidia elegans, Galidictis fasciata, Gymnuromys roberti, Hapalemur aureus, Lepilemur microdon, Microcebus rufus, Microgale drouhardi, Microgale majori, Microgale parvula, Microgale taiva, Microgale thomasi, Nesomys rufus, Propithecus edwardsi, Tenrec ecaudatus, Varecia varecia*
9	Andringitra – Subhumid [c]	*Avahi laniger, Brachyuromys ramirohitra, Cheirogaleus major, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus majori, Eliurus minor, Eliurus tanala, Eulemur cinereiceps, Eulemur fulvus, Eulemur rubriventer, Eulemur rufifrons, Eupleres goudotii, Fossa fossana, Galidia elegans, Gymnuromys roberti, Hapalemur aureus, Hapalemur griseus, Lepilemur microdon, Limnogale mergulus, Microcebus rufus, Microgale cowani, Microgale dobsoni, Microgale drouhardi, Microgale fotsifotsy, Microgale gracilis, Microgale gymnorhyncha, Microgale majori, Microgale parvula, Microgale pusilla, Microgale soricoides, Microgale taiva, Microgale thomasi, Monticolomys koopmani, Nesomys rufus, Prolemur simus, Setifer setosus, Tenrec ecaudatus, Varecia varecia*
10	Anjanaharibe Sud	*Allocebus trichotis, Avahi laniger, Brachytarsomys albicauda, Brachytarsomys villosa, Brachyuromys betsileoensis, Cheirogaleus crossleyi, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus grandidieri, Eliurus majori, Eliurus minor, Eliurus tanala, Eliurus webbi, Eulemur albifrons, Eulemur rubriventer, Fossa fossana, Galidia elegans, Gymnuromys roberti, Hapalemur griseus, Hemicentetes semispinosus, Indri indri, Lepilemur seali,*

Site ID#	Site	Species Occurrence [b]
		Microcebus mittermeieri, Microgale cowani, Microgale dobsoni, Microgale fotsifotsy, Microgale gracilis, Microgale gymnorhyncha, Microgale longicaudata, Microgale monticola, Microgale parvula, Microgale principula, Microgale soricoides, Microgale taiva, Microgale talazaci, Nesomys rufus, Oryzorictes hova, Propithecus candidus, Setifer setosus, Tenrec ecaudatus, Voalavo gymnocaudus
11	Anjozorobe	*Avahi laniger, Brachytarsomys albicauda, Cheirogaleus crossleyi, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus grandidieri, Eliurus majori, Eliurus minor, Eliurus tanala, Eulemur fulvus, Eulemur rubriventer, Eupleres goudotii, Fossa fossana, Galidia elegans, Galidictis fasciata, Gymnuromys roberti, Hapalemur griseus, Hemicentetes nigriceps, Hemicentetes semispinosus, Indri indri, Lepilemur mustelinus, Microcebus rufus, Microgale cowani, Microgale dobsoni, Microgale fotsifotsy, Microgale gymnorhyncha, Microgale longicaudata, Microgale majori, Microgale parvula, Microgale principula, Microgale soricoides, Microgale taiva, Microgale talazaci, Microgale thomasi, Nesomys rufus, Oryzorictes hova, Propithecus diadema, Setifer setosus, Tenrec ecaudatus, Varecia varecia, Voalavo antsahabensis*
12	Ankarafantsika	*Avahi occidentalis, Cheirogaleus crossleyi, Cheirogaleus medius, Cryptoprocta ferox, Eliurus minor, Eliurus myoxinus, Eulemur fulvus, Eulemur mongoz, Eupleres goudotii, Lepilemur edwardsi, Macrotarsomys bastardi, Macrotarsomys ingens, Microcebus murinus, Microcebus ravelobensis, Microgale brevicaudata, Propithecus coquereli, Setifer setosus, Tenrec ecaudatus*
13	Ankarana	*Avahi occidentalis, Cheirogaleus crossleyi, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus carletoni, Eliurus myoxinus, Eulemur coronatus, Eulemur sanfordi, Eupleres goudotii, Fossa fossana, Galidia elegans, Hapalemur occidentalis, Lepilemur ankaranensis, Microcebus murinus, Microcebus tavaratra, Microgale brevicaudata, Phaner electromontis, Propithecus perrieri, Setifer setosus, Tenrec ecaudatus*
14	Bemaraha	*Avahi cleesei, Cheirogaleus medius, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus antsingy, Eliurus myoxinus, Eliurus tanala, Eulemur rufus, Galidia elegans, Hapalemur occidentalis, Lepilemur randrianasoli, Microcebus murinus, Microcebus myoxinus, Microgale grandidieri, Mirza coquereli, Nesomys lambertoni, Phaner pallescens, Propithecus deckenii, Setifer setosus, Tenrec ecaudatus*
15	Berenty	*Cheirogaleus medius, Cryptoprocta ferox, Echinops telfairi, Eliurus myoxinus, Eulemur*

Site ID#	Site	Species Occurrence [b]
		rufifrons, Geogale aurita, Lemur catta, Lepilemur leucopus, Microcebus griseorufus, Microcebus murinus, Propithecus verreauxi, Setifer setosus, Tenrec ecaudatus
16	Beza Mahafaly	*Cryptoprocta ferox, Echinops telfairi, Eliurus myoxinus, Geogale aurita, Lemur catta, Lepilemur petteri, Macrotarsomys bastardi, Microcebus griseorufus, Propithecus verreauxi, Setifer setosus, Tenrec ecaudatus*
17	Forêt des Mikea	*Cheirogaleus medius, Cryptoprocta ferox, Echinops telfairi, Eulemur rufus, Geogale aurita, Lemur catta, Lepilemur ruficaudatus, Macrotarsomys bastardi, Macrotarsomys petteri, Microcebus griseorufus, Microcebus murinus, Microgale jenkinsae*
18	Isalo	*Cheirogaleus medius, Cryptoprocta ferox, Eliurus danieli, Eliurus myoxinus, Eulemur rufifrons, Lemur catta, Lepilemur ruficaudatus, Microcebus murinus, Mirza coquereli, Propithecus verreauxi, Setifer setosus, Tenrec ecaudatus*
19	Kirindy CFPF	*Cheirogaleus medius, Cryptoprocta ferox, Echinops telfairi, Eliurus myoxinus, Eulemur rufus, Geogale aurita, Hypogeomys antimena, Lepilemur ruficaudatus, Macrotarsomys bastardi, Microcebus berthae, Microcebus murinus, Microgale brevicaudata, Microgale majori, Microgale nasoloi, Mirza coquereli, Mungotictis decemlineata, Phaner pallescens, Propithecus verreauxi, Setifer setosus, Tenrec ecaudatus*
20	Kirindy Mitea	*Cheirogaleus medius, Cryptoprocta ferox, Echinops telfairi, Eliurus myoxinus, Eulemur rufifrons, Geogale aurita, Lemur catta, Lepilemur ruficaudatus, Macrotarsomys bastardi, Microcebus murinus, Microgale brevicaudata, Mirza coquereli, Mungotictis decemlineata, Phaner pallescens, Propithecus verreauxi, Setifer setosus, Tenrec ecaudatus*
21	Manongarivo	*Avahi unicolor, Cheirogaleus crossleyi, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus grandidieri, Eliurus majori, Eliurus minor, Eliurus myoxinus, Eliurus webbi, Eulemur fulvus, Eulemur macaco, Eupleres goudotii, Fossa fossana, Galidia elegans, Hapalemur occidentalis, Lepilemur dorsalis, Microcebus sambiranensis, Microgale brevicaudata, Microgale cowani, Microgale dobsoni, Microgale drouhardi, Microgale fotsifotsy, Microgale longicaudata, Microgale majori, Microgale soricoides, Microgale talazaci, Nesomys rufus, Oryzorictes hova, Phaner parienti, Setifer setosus, Tenrec ecaudatus*
22	Mantadia	*Allocebus trichotis, Avahi laniger, Cheirogaleus crossleyi, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus tanala, Eulemur fulvus, Eulemur rubriventer, Eupleres goudotii, Fossa fossana, Galidia elegans, Galidictis fasciata, Gymnuromys roberti, Hapalemur griseus,*

Site ID#	Site	Species Occurrence [b]
		Hemicentetes semispinosus, Indri indri, Lepilemur mustelinus, Microcebus lehilahytsara, Microgale cowani, Microgale drouhardi, Microgale longicaudata, Microgale parvula, Microgale principula, Microgale soricoides, Microgale taiva, Microgale talazaci, Microgale thomasi, Nesomys rufus, Propithecus diadema, Setifer setosus, Tenrec ecaudatus, Varecia varecia
23	Marojejy – Humid [c]	*Avahi laniger, Brachytarsomys albicauda, Cheirogaleus crossleyi, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus minor, Eliurus tanala, Eliurus webbi, Eulemur albifrons, Eulemur rubriventer, Eupleres goudotii, Fossa fossana, Hapalemur griseus, Hemicentetes semispinosus, Lepilemur mustelinus, Microcebus mittermeieri, Microgale brevicaudata, Microgale parvula, Microgale talazaci, Nesomys rufus, Oryzorictes hova, Phaner electromontis, Setifer setosus, Tenrec ecaudatus*
24	Marojejy – Subhumid [c]	*Allocebus trichotis, Avahi laniger, Brachytarsomys albicauda, Cheirogaleus crossleyi, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus grandidieri, Eliurus majori, Eliurus minor, Eliurus myoxinus, Eliurus tanala, Eulemur albifrons, Eulemur rubriventer, Galidia elegans, Gymnuromys roberti, Hapalemur griseus, Hemicentetes semispinosus, Lepilemur mustelinus, Microcebus mittermeieri, Microgale brevicaudata, Microgale cowani, Microgale dobsoni, Microgale fotsifotsy, Microgale gracilis, Microgale gymnorhyncha, Microgale longicaudata, Microgale monticola, Microgale parvula, Microgale principula, Microgale soricoides, Microgale taiva, Microgale talazaci, Nesomys rufus, Oryzorictes hova, Propithecus candidus, Setifer setosus, Voalavo gymnocaudus*
25	Masoala	*Allocebus trichotis, Avahi mooreorum, Cheirogaleus major, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus minor, Eliurus webbi, Eulemur albifrons, Eupleres goudotii, Fossa fossana, Galidia elegans, Galidictis fasciata, Hapalemur griseus, Hemicentetes semispinosus, Lepilemur scottorum, Microcebus rufus, Microgale brevicaudata, Microgale cowani, Microgale dobsoni, Microgale parvula, Microgale taiva, Microgale talazaci, Nesomys audeberti, Nesomys rufus, Oryzorictes hova, Phaner furcifer, Salanoia concolor, Setifer setosus, Tenrec ecaudatus, Varecia varecia*
26	Montagne d'Ambre	*Cheirogaleus crossleyi, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus majori, Eliurus minor, Eliurus webbi, Eulemur coronatus, Eulemur sanfordi, Eupleres goudotii, Fossa fossana, Galidia elegans, Lepilemur septentrionalis, Microcebus arnholdi, Microgale*

Site ID#	Site	Species Occurrence [b]
		brevicaudata, Microgale cowani, Microgale drouhardi, Microgale fotsifotsy, Microgale longicaudata, Microgale parvula, Microgale talazaci, Phaner electromontis, Setifer setosus, Tenrec ecaudatus
27	Namoroka	*Cheirogaleus medius, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus antsingy, Eliurus myoxinus, Eulemur rufus, Galidia elegans, Hapalemur occidentalis, Lepilemur edwardsi, Microcebus murinus, Microcebus myoxinus, Microgale grandidieri, Mirza coquereli, Phaner pallescens, Propithecus deckenii, Setifer setosus, Tenrec ecaudatus*
28	Ranomafana	*Avahi laniger, Avahi peyrierasi, Brachytarsomys albicauda, Brachyuromys betsileoensis, Cheirogaleus crossleyi, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus majori, Eliurus minor, Eliurus tanala, Eliurus webbi, Eulemur rubriventer, Eulemur rufifrons, Eupleres goudotii, Fossa fossana, Galidia elegans, Galidictis fasciata, Gymnuromys roberti, Hapalemur aureus, Hapalemur griseus, Hemicentetes semispinosus, Lepilemur microdon, Limnogale mergulus, Microcebus rufus, Microgale cowani, Microgale fotsifotsy, Microgale gracilis, Microgale gymnorhyncha, Microgale longicaudata, Microgale principula, Microgale soricoides, Microgale taiva, Microgale talazaci, Microgale thomasi, Monticolomys koopmani, Nesomys audeberti, Nesomys rufus, Prolemur simus, Propithecus edwardsi, Setifer setosus, Tenrec ecaudatus, Varecia varecia*
29	Tsaratanana	*Brachytarsomys villosa, Cheirogaleus crossleyi, Daubentonia madagascariensis, Eliurus grandidieri, Eliurus majori, Eliurus minor, Eliurus tanala, Eliurus webbi, Eulemur fulvus, Eulemur macaco, Eupleres goudotii, Galidia elegans, Hapalemur griseus, Hemicentetes semispinosus, Lepilemur mustelinus, Microgale brevicaudata, Microgale cowani, Microgale dobsoni, Microgale drouhardi, Microgale fotsifotsy, Microgale gymnorhyncha, Microgale jobihely, Microgale longicaudata, Microgale majori, Microgale parvula, Microgale soricoides, Microgale taiva, Microgale talazaci, Monticolomys koopmani, Nesomys rufus, Oryzorictes hova, Phaner parienti, Setifer setosus, Tenrec ecaudatus*
30	Tsimanampesotse	*Cryptoprocta ferox, Echinops telfairi, Eliurus myoxinus, Galidictis grandidieri, Geogale aurita, Lemur catta, Lepilemur petteri, Macrotarsomys bastardi, Microcebus griseorufus, Microcebus murinus, Propithecus verreauxi, Setifer setosus, Tenrec ecaudatus*
31	Tsinjoarivo	*Avahi laniger, Cheirogaleus crossleyi, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus grandidieri, Eliurus majori, Eliurus minor, Eulemur fulvus, Eulemur rubriventer, Fossa*

Site ID#	Site	Species Occurrence [b]
		fossana, Galidia elegans, Galidictis fasciata, Gymnuromys roberti, Hapalemur griseus, Hemicentetes nigriceps, Hemicentetes semispinosus, Lepilemur mustelinus, Microcebus rufus, Microgale cowani, Microgale dobsoni, Microgale fotsifotsy, Microgale gracilis, Microgale gymnorhyncha, Microgale longicaudata, Microgale parvula, Microgale pusilla, Microgale soricoides, Microgale taiva, Microgale thomasi, Nesomys rufus, Oryzorictes hova, Propithecus diadema, Setifer setosus, Tenrec ecaudatus, Varecia varecia
32	Verezanantsoro	*Allocebus trichotis, Avahi laniger, Cheirogaleus major, Cryptoprocta ferox, Daubentonia madagascariensis, Eliurus grandidieri, Eliurus minor, Eliurus tanala, Eliurus webbi, Eulemur albifrons, Eupleres goudotii, Fossa fossana, Galidia elegans, Galidictis fasciata, Hapalemur griseus, Hemicentetes semispinosus, Indri indri, Lepilemur hollandorum, Microcebus rufus, Microgale dobsoni, Microgale fotsifotsy, Microgale parvula, Microgale principula, Nesomys rufus, Oryzorictes hova, Propithecus diadema, Salanoia concolor, Setifer setosus, Tenrec ecaudatus, Varecia varecia*
33	Zahamena	*Allocebus trichotis, Avahi laniger, Cheirogaleus crossleyi, Cryptoprocta ferox, Eliurus minor, Eulemur albifrons, Eulemur rubriventer, Eupleres goudotii, Fossa fossana, Galidia elegans, Galidictis fasciata, Hapalemur griseus, Indri indri, Lepilemur mustelinus, Microcebus simmonsi, Microgale drouhardi, Microgale fotsifotsy, Microgale parvula, Phaner furcifer, Propithecus diadema, Salanoia concolor, Setifer setosus, Tenrec ecaudatus, Varecia varecia*
34	Zombitse Vohibasia	*Cheirogaleus medius, Cryptoprocta ferox, Echinops telfairi, Eliurus myoxinus, Eulemur rufifrons, Geogale aurita, Lemur catta, Lepilemur hubbardi, Macrotarsomys bastardi, Microcebus murinus, Microgale nasoloi, Mirza coquereli, Phaner pallescens, Propithecus verreauxi, Setifer setosus, Tenrec ecaudatus*

[a] *Sensu* Muldoon and Goodman (2010) Family Soricidae not included due to limited data.

[b] Compiled from: Alonso et al. 2002; Andriaholinirina et al. 2006; Andrianjakarivelo et al. 2005; Andriantompohavana et al. 2007; Blanco et al. 2009; Bousquet and Rabetaliana 1992; Carleton and Goodman 1996, 1998, 2000, 2007; Carleton et al. 2001; Conservation Breeding Specialist Group 2002; Craul et al. 2007; Duckworth and Rakotondraparany 1990; Feistner and Schmid 1999; Goodman 1996, 1998, 1999, 2000; Goodman and Carleton 1998; Goodman and Jenkins 1998, 2000; Goodman and Langrand 1994; Goodman and Raselimanana 2002; Goodman and Rasolonandrasana 1999, 2001; Goodman and Razafindratsita 2001; Goodman and Schütz 1999; Goodman and Soarimalala 2002, 2005; Goodman and Wilmé 2003, 2006; Goodman et al. 1996; Goodman et al. 1997a, 1997b, 2003, 2005, 2008, 2009; Hawkins 1999; Hawkins et al. 1990; Hawkins and Racey 2008; Heckman et al. 2006; Jenkins 1993;

Jenkins and Goodman 1999; Kappeler et al. 2005; Langrand and Goodman 1997; Lei et al. 2008; Louis et al. 2006, 2008; Mahazotahy et al. 2006; Maminirina et al. 2008; Olivieri et al. 2007; Olson et al. 2009; Radespiel et al. 2006, 2008; Rakotondraparany and Medard 2005; Rakotondravony et al. 1998, 2002; Ralison 2008; Ramaromilato et al. 2009; Randrianarisoa et al. 2001; Randriatahina nad Rabarivola 2004; Raselimanana and Goodman 2004; Rasoloarison et al. 2000; Ratsirarson and Goodman 2000; Raxworthy and Rakotondraparany 1988; Schmid and Alonso 2005; Schmid and Smolker 1998; Schmid et al. 2005; Soarimalala 2008; Soarimalala and Goodman 2008; Stephenson 1993, 1994; Stephenson et al. 1994; Sterling and McFadden 2000; Thalmann and Geissmann 2005; Thomas et al. 2005; Vasey 2000; Wilmé e tal. 2012; Yoder et al. 2002; Youssouf and Rasoazanabary 2008

[c] cf. Muldoon and Goodman 2010 classification: Humid forest (0-800 m), Subhumid forest (800-1600 m)

Table A.2. Australian occurrence data for all non-volant mammal species included in analyses. Publication cut-off date for included sources of information was January 2012. * indicate Australian sites with ≥ 5 arboreal mammal species.

Site ID#	Site	Species List [a]
1*	Abercrombie River	*Acrobates pygmaeus, Antechinus stuartii, Cercartetus nanus, Dasyurus hallucatus, Macropus giganteus, Macropus rufogriseus, Petauroides volans, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Phascolarctos cinereus, Pseudocheirus peregrinus, Tachyglossus aculeatus, Trichosurus vulpecula, Vombatus ursinus, Wallabia bicolor*
2*	Arakoon	*Aepyprymnus rufescens, Cercartetus nanus, Dasyurus hallucatus, Macropus parma, Perameles nasuta, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Petrogale penicillata, Phascogale tapoatafa, Phascolarctos cinereus, Planigale maculata, Potorous tridactylus, Pseudocheirus peregrinus, Pseudomys gracilicaudatus, Rattus fuscipes, Tachyglossus aculeatus, Thylogale stigmatica, Wallabia bicolor*
3*	Arakwal	*Aepyprymnus rufescens, Cercartetus nanus, Dasyurus hallucatus, Macropus dorsalis, Macropus parma, Perameles nasuta, Petaurus australis, Petaurus norfolcensis, Petrogale penicillata, Phascogale tapoatafa, Phascolarctos cinereus, Planigale maculata, Potorous tridactylus, Pseudomys gracilicaudatus, Pseudomys novaehollandiae, Pseudomys oralis, Rattus fuscipes, Rattus lutreolus, Thylogale stigmatica, Trichosurus caninus, Wallabia bicolor*
4*	Bangadilly	*Cercartetus nanus, Dasyurus hallucatus, Isoodon obesulus, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Petrogale penicillata, Phascolarctos cinereus, Pseudomys novaehollandiae*
5	Blackbraes	*Aepyprymnus rufescens, Isoodon macrourus, Lagorchestes conspicillatus, Macropus giganteus, Macropus robustus, Petauroides volans, Petaurus breviceps, Petrogale assimilis, Phascolarctos cinereus, Pseudomys gracilicaudatus, Sminthopsis archeri, Tachyglossus aculeatus, Trichosurus vulpecula*
6	Bladensburg	*Macropus giganteus, Macropus robustus, Macropus rufus, Planigale ingrami, Pseudomys hermannsburgensis, Sminthopsis douglasi, Tachyglossus aculeatus, Trichosurus vulpecula, Zyzomys argurus*
7*	Blue Mountains	*Acrobates pygmaeus, Antechinus flavipes, Antechinus stuartii, Antechinus swainsonii, Cercartetus nanus, Dasyurus hallucatus, Hydromys chrysogaster, Isoodon obesulus, Macropus giganteus, Macropus parma, Macropus robustus, Macropus rufogriseus, Petauroides volans, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Petrogale penicillata, Phascogale tapoatafa,*

Site ID#	Site	Species List [a]
		Phascolarctos cinereus, Pseudocheirus peregrinus, Pseudomys novaehollandiae, Rattus fuscipes, Rattus lutreolus, Sminthopsis murina, Tachyglossus aculeatus, Trichosurus vulpecula, Vombatus ursinus, Wallabia bicolor
8	Boodjamulla Lawn Hill	*Macropus agilis, Macropus antilopinus, Macropus robustus, Petrogale purpureicollis, Petropseudes dahli, Planigale ingrami, Pseudomys delicatulus, Pseudomys desertor, Pseudomys nanus, Rattus villosissimus, Sminthopsis macroura, Tachyglossus aculeatus, Zyzomys argurus*
9*	Border Ranges	*Acrobates pygmaeus, Aepyprymnus rufescens, Antechinus flavipes, Antechinus stuartii, Antechinus subtropicus, Antechinus swainsonii, Cercartetus nanus, Hydromys chrysogaster, Isoodon macrourus, Macropus dorsalis, Macropus parma, Melomys cervinipes, Petauroides volans, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Petrogale penicillata, Phascogale tapoatafa, Phascolarctos cinereus, Planigale maculata, Potorous tridactylus, Pseudocheirus peregrinus, Pseudomys gracilicaudatus, Pseudomys novaehollandiae, Pseudomys oralis, Rattus fuscipes, Rattus lutreolus, Sminthopsis murina, Tachyglossus aculeatus, Thylogale stigmatica, Thylogale thetis, Trichosurus caninus, Trichosurus vulpecula, Wallabia bicolor*
10	Cape Melville	*Dasyurus hallucatus, Macropus agilis, Macropus giganteus, Melomys burtoni, Melomys capensis, Phascogale tapoatafa, Uromys caudimaculatus*
11*	Carnarvon	*Aepyprymnus rufescens, Antechinus flavipes, Dasyurus hallucatus, Hydromys chrysogaster, Isoodon macrourus, Macropus dorsalis, Macropus giganteus, Macropus parryi, Macropus robustus, Macropus rufogriseus, Macropus rufus, Melomys cervinipes, Ornithorhynchus anatinus, Petauroides volans, Petaurus australis, Petaurus norfolcensis, Petrogale penicillata, Phascolarctos cinereus, Planigale maculata, Planigale tenuirostris, Pseudocheirus peregrinus, Pseudomys delicatulus, Pseudomys gracilicaudatus, Pseudomys patrius, Rattus fuscipes, Rattus tunneyi, Sminthopsis murina, Tachyglossus aculeatus, Trichosurus vulpecula, Wallabia bicolor*
12*	Carrai	*Aepyprymnus rufescens, Antechinus flavipes, Antechinus stuartii, Antechinus swainsonii, Cercartetus nanus, Dasyurus hallucatus, Hydromys chrysogaster, Isoodon macrourus, Macropus giganteus, Macropus parma, Macropus rufogriseus, Melomys cervinipes, Perameles nasuta, Petauroides volans, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Petrogale penicillata, Phascogale tapoatafa, Phascolarctos cinereus, Planigale maculata, Potorous tridactylus, Pseudocheirus peregrinus, Pseudomys gracilicaudatus, Pseudomys novaehollandiae, Pseudomys oralis, Rattus fuscipes, Rattus lutreolus, Thylogale stigmatica, Thylogale thetis, Trichosurus caninus,*

Site ID#	Site	Species List [a]
		Wallabia bicolor
13*	Chiltern MtPilot	*Acrobates pygmaeus, Antechinus agilis, Antechinus flavipes, Cercartetus nanus, Dasyurus maculatus, Macropus giganteus, Perameles nasuta, Petaurus breviceps, Petaurus norfolcensis, Phascogale tapoatafa, Phascolarctos cinereus, Pseudocheirus peregrinus, Tachyglossus aculeatus, Trichosurus vulpecula, Vombatus ursinus, Wallabia bicolor*
14	Currawinya	*Antechinomys laniger, Hydromys chrysogaster, Macropus fuliginosus, Macropus giganteus, Macropus robustus, Macropus rufus, Sminthopsis crassicaudata*
15*	Daintree	*Acrobates pygmaeus, Antechinus flavipes, Dactylopsila trivirgata, Dasyurus hallucatus, Dendrolagus bennettianus, Hydromys chrysogaster, Hypsiprymnodon moschatus, Isoodon macrourus, Melomys cervinipes, Perameles nasuta, Petauroides volans, Petaurus australis, Petaurus breviceps, Pseudocheirus peregrinus, Pseudochirulus cinereus, Rattus lutreolus, Thylogale stigmatica, Trichosurus vulpecula, Uromys caudimaculatus*
16	Diamantina	*Antechinomys laniger, Dasyuroides byrnei, Leggadina forresti, Macropus robustus, Macropus rufus, Macrotis lagotis, Notomys cervinus, Petrogale inornata, Planigale ingrami, Planigale tenuirostris, Pseudomys desertor, Pseudomys hermannsburgensis, Rattus villosissimus, Sminthopsis crassicaudata, Sminthopsis macroura, Tachyglossus aculeatus*
17*	Dunggir	*Aepyprymnus rufescens, Antechinus flavipes, Antechinus stuartii, Cercartetus nanus, Dasyurus hallucatus, Macropus parma, Perameles nasuta, Petauroides volans, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Petrogale penicillata, Phascogale tapoatafa, Phascolarctos cinereus, Planigale maculata, Potorous tridactylus, Pseudomys gracilicaudatus, Pseudomys novaehollandiae, Pseudomys oralis, Rattus fuscipes, Sminthopsis murina, Thylogale stigmatica, Thylogale thetis, Trichosurus caninus, Wallabia bicolor*
18*	Eungella	*Acrobates pygmaeus, Antechinus flavipes, Antechinus subtropicus, Dasyurus hallucatus, Hydromys chrysogaster, Isoodon macrourus, Melomys cervinipes, Perameles nasuta, Petauroides volans, Petaurus breviceps, Petaurus norfolcensis, Planigale maculata, Pseudocheirus peregrinus, Rattus lutreolus, Tachyglossus aculeatus, Trichosurus vulpecula, Zyzomys argurus*
19	Expedition Limited Depth	*Acrobates pygmaeus, Aepyprymnus rufescens, Hydromys chrysogaster, Macropus dorsalis, Macropus giganteus, Macropus parryi, Macropus robustus, Petauroides volans, Petaurus breviceps, Petrogale herberti, Rattus fuscipes, Tachyglossus aculeatus, Wallabia bicolor*
20	Forest Den	*Macropus giganteus, Macropus rufus, Planigale maculata, Planigale tenuirostris, Pseudomys*

Site ID#	Site	Species List [a]
		hermannsburgensis, Sminthopsis macroura, Tachyglossus aculeatus, Trichosurus vulpecula
21*	Gibraltar Range	*Acrobates pygmaeus, Aepyprymnus rufescens, Antechinus stuartii, Cercartetus nanus, Dasyurus hallucatus, Isoodon macrourus, Macropus parma, Macropus rufogriseus, Melomys cervinipes, Perameles nasuta, Petauroides volans, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Petrogale penicillata, Phascogale tapoatafa, Phascolarctos cinereus, Planigale maculata, Potorous tridactylus, Pseudocheirus peregrinus, Pseudomys gracilicaudatus, Pseudomys novaehollandiae, Pseudomys oralis, Rattus fuscipes, Rattus lutreolus, Tachyglossus aculeatus, Thylogale thetis, Trichosurus caninus, Wallabia bicolor*
22*	Girringun	*Acrobates pygmaeus, Antechinus adustus, Antechinus flavipes, Antechinus godmani, Dactylopsila trivirgata, Dasyurus hallucatus, Dendrolagus lumholtzi, Hydromys chrysogaster, Hypsiprymnodon moschatus, Isoodon macrourus, Macropus agilis, Macropus giganteus, Macropus parryi, Macropus robustus, Melomys burtoni, Melomys cervinipes, Perameles nasuta, Petauroides volans, Petaurus gracilis, Petaurus norfolcensis, Phascolarctos cinereus, Pseudocheirus peregrinus, Pseudochirops archeri, Pseudochirulus herbertensis, Pseudomys gracilicaudatus, Rattus fuscipes, Rattus lutreolus, Rattus sordidus, Sminthopsis virginiae, Tachyglossus aculeatus, Thylogale stigmatica, Trichosurus vulpecula, Uromys caudimaculatus, Zyzomys argurus*
23*	Great Sandy	*Acrobates pygmaeus, Aepyprymnus rufescens, Antechinus flavipes, Dasyurus hallucatus, Hydromys chrysogaster, Macropus giganteus, Melomys burtoni, Melomys cervinipes, Perameles nasuta, Petauroides volans, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Phascolarctos cinereus, Planigale maculata, Potorous tridactylus, Pseudocheirus peregrinus, Pseudomys gracilicaudatus, Rattus fuscipes, Rattus lutreolus, Rattus tunneyi, Sminthopsis murina, Tachyglossus aculeatus, Trichosurus caninus, Trichosurus vulpecula, Wallabia bicolor, Xeromys myoides*
24*	Gumbaynggirr	*Aepyprymnus rufescens, Cercartetus nanus, Dasyurus hallucatus, Macropus parma, Melomys cervinipes, Perameles nasuta, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Petrogale penicillata, Phascogale tapoatafa, Phascolarctos cinereus, Planigale maculata, Potorous tridactylus, Pseudomys gracilicaudatus, Pseudomys novaehollandiae, Pseudomys oralis, Rattus fuscipes, Thylogale stigmatica*
25	Gundabooka	*Antechinomys laniger, Dasyurus hallucatus, Leporillus conditor, Macropus fuliginosus, Macropus giganteus, Macropus robustus, Macropus rufus, Petrogale penicillata, Phascolarctos cinereus, Sminthopsis crassicaudata, Sminthopsis macroura, Sminthopsis murina, Tachyglossus aculeatus,*

Site ID#	Site	Species List [a]
		Trichosurus vulpecula
26*	Guy Fawkes River	*Acrobates pygmaeus, Aepyprymnus rufescens, Antechinus stuartii, Cercartetus nanus, Dasyurus hallucatus, Hydromys chrysogaster, Isoodon macrourus, Macropus giganteus, Macropus parma, Macropus parryi, Macropus robustus, Macropus rufogriseus, Melomys cervinipes, Perameles nasuta, Petauroides volans, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Petrogale penicillata, Phascogale tapoatafa, Phascolarctos cinereus, Planigale maculata, Potorous tridactylus, Pseudocheirus peregrinus, Pseudomys gracilicaudatus, Pseudomys novaehollandiae, Pseudomys oralis, Rattus fuscipes, Rattus lutreolus, Sminthopsis murina, Tachyglossus aculeatus, Thylogale stigmatica, Thylogale thetis, Trichosurus caninus, Trichosurus vulpecula, Vombatus ursinus, Wallabia bicolor*
27*	HerbertonRange	*Dactylopsila trivirgata, Dendrolagus lumholtzi, Hemibelideus lemuroides, Melomys cervinipes, Petaurus breviceps, Pseudochirulus herbertensis*
28	Idalia	*Antechinomys laniger, Hydromys chrysogaster, Macropus dorsalis, Macropus giganteus, Macropus robustus, Macropus rufus, Onychogalea fraenata, Petrogale xanthopus, Phascolarctos cinereus, Rattus villosissimus, Sminthopsis macroura, Tachyglossus aculeatus, Trichosurus vulpecula, Wallabia bicolor*
29	Jardine River	*Melomys burtoni, Melomys capensis, Rattus leucopus, Rattus sordidus, Rattus tunneyi, Thylogale stigmatica*
30	Kakadu	*Conilurus penicillatus, Isoodon auratus, Isoodon macrourus, Macropus antilopinus, Melomys burtoni, Petrogale brachyotis, Pseudomys gracilicaudatus, Trichosurus vulpecula*
31	Kinchega	*Antechinomys laniger, Hydromys chrysogaster, Macropus fuliginosus, Macropus giganteus, Macropus robustus, Macropus rufus, Planigale gilesi, Planigale tenuirostris, Sminthopsis crassicaudata, Sminthopsis macroura, Tachyglossus aculeatus, Trichosurus vulpecula*
32*	Kirrama	*Antechinus adustus, Hemibelideus lemuroides, Melomys cervinipes, Perameles nasuta, Pseudochirops archeri, Pseudochirulus herbertensis, Rattus fuscipes, Thylogale stigmatica, Uromys caudimaculatus*
33*	Lamington	*Antechinus flavipes, Antechinus stuartii, Antechinus subtropicus, Antechinus swainsonii, Cercartetus nanus, Dasyurus hallucatus, Hydromys chrysogaster, Isoodon macrourus, Macropus giganteus, Macropus parryi, Melomys cervinipes, Perameles nasuta, Petaurus australis, Petaurus breviceps, Phascogale tapoatafa, Phascolarctos cinereus, Planigale maculata, Potorous tridactylus,*

Site ID#	Site	Species List [a]
		Pseudocheirus peregrinus, Pseudomys gracilicaudatus, Pseudomys oralis, Rattus fuscipes, Rattus lutreolus, Tachyglossus aculeatus, Thylogale stigmatica, Thylogale thetis, Trichosurus caninus, Trichosurus vulpecula, Wallabia bicolor
34	Mallee Cliffs	*Cercartetus concinnus, Macropus fuliginosus, Macropus rufus, Ningaui yvonnae, Pseudomys bolami, Sminthopsis crassicaudata, Sminthopsis murina, Tachyglossus aculeatus, Trichosurus vulpecula*
35*	Mebbin	*Aepyprymnus rufescens, Antechinus stuartii, Cercartetus nanus, Dasyurus hallucatus, Isoodon macrourus, Macropus dorsalis, Macropus parma, Melomys cervinipes, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Petrogale penicillata, Phascogale tapoatafa, Phascolarctos cinereus, Planigale maculata, Potorous tridactylus, Pseudocheirus peregrinus, Pseudomys gracilicaudatus, Pseudomys novaehollandiae, Pseudomys oralis, Rattus fuscipes, Thylogale stigmatica, Thylogale thetis, Trichosurus caninus*
36*	Mitchell Plateau	*Acrobates pygmaeus, Antechinus flavipes, Antechinus stuartii, Antechinus swainsonii, Cercartetus nanus, Hydromys chrysogaster, Isoodon obesulus, Macropus fuliginosus, Macropus giganteus, Macropus rufogriseus, Petaurus breviceps, Petrogale penicillata, Phascolarctos cinereus, Potorous tridactylus, Pseudocheirus peregrinus, Pseudomys fumeus, Pseudomys shortridgei, Rattus lutreolus, Tachyglossus aculeatus, Trichosurus vulpecula, Wallabia bicolor*
37*	Morton	*Acrobates pygmaeus, Antechinus stuartii, Antechinus swainsonii, Cercartetus nanus, Dasyurus hallucatus, Macropus giganteus, Macropus parma, Macropus robustus, Macropus rufogriseus, Perameles nasuta, Petauroides volans, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Petrogale penicillata, Phascogale tapoatafa, Phascolarctos cinereus, Potorous longipes, Potorous tridactylus, Pseudocheirus peregrinus, Pseudomys fumeus, Pseudomys gracilicaudatus, Pseudomys novaehollandiae, Rattus fuscipes, Rattus lutreolus, Sminthopsis leucopus, Sminthopsis murina, Tachyglossus aculeatus, Trichosurus caninus, Trichosurus vulpecula, Vombatus ursinus, Wallabia bicolor*
38	Mungo	*Cercartetus concinnus, Macropus fuliginosus, Macropus giganteus, Macropus rufus, Ningaui yvonnae, Planigale tenuirostris, Pseudomys bolami, Rattus villosissimus, Sminthopsis crassicaudata, Sminthopsis murina, Tachyglossus aculeatus*
39*	Myall Lakes	*Acrobates pygmaeus, Aepyprymnus rufescens, Antechinus flavipes, Antechinus stuartii, Antechinus swainsonii, Cercartetus nanus, Dasyurus hallucatus, Hydromys chrysogaster, Isoodon macrourus,*

Site ID#	Site	Species List [a]
		Macropus giganteus, Macropus parma, Macropus rufogriseus, Ornithorhynchus anatinus, Perameles nasuta, Petauroides volans, Petaurus australis, Petaurus breviceps, Petrogale penicillata, Phascogale tapoatafa, Phascolarctos cinereus, Planigale maculata, Potorous tridactylus, Pseudocheirus peregrinus, Pseudomys gracilicaudatus, Pseudomys novaehollandiae, Rattus fuscipes, Rattus lutreolus, Sminthopsis murina, Tachyglossus aculeatus, Thylogale stigmatica, Thylogale thetis, Trichosurus caninus, Trichosurus vulpecula, Vombatus ursinus, Wallabia bicolor
40*	New England	*Aepyprymnus rufescens, Antechinus stuartii, Antechinus swainsonii, Cercartetus nanus, Dasyurus hallucatus, Isoodon macrourus, Macropus giganteus, Macropus parma, Macropus rufogriseus, Melomys cervinipes, Perameles nasuta, Petauroides volans, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Petrogale penicillata, Phascogale tapoatafa, Phascolarctos cinereus, Planigale maculata, Potorous tridactylus, Pseudocheirus peregrinus, Pseudomys gracilicaudatus, Pseudomys novaehollandiae, Pseudomys oralis, Rattus fuscipes, Tachyglossus aculeatus, Thylogale stigmatica, Thylogale thetis, Trichosurus caninus, Wallabia bicolor*
41*	Oxley Wild Rivers	*Acrobates pygmaeus, Aepyprymnus rufescens, Antechinus stuartii, Antechinus swainsonii, Cercartetus nanus, Dasyurus hallucatus, Hydromys chrysogaster, Isoodon macrourus, Macropus giganteus, Macropus parma, Macropus robustus, Macropus rufogriseus, Melomys cervinipes, Perameles nasuta, Petauroides volans, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Petrogale penicillata, Phascogale tapoatafa, Phascolarctos cinereus, Planigale maculata, Potorous tridactylus, Pseudocheirus peregrinus, Pseudomys gracilicaudatus, Pseudomys novaehollandiae, Pseudomys oralis, Rattus fuscipes, Sminthopsis murina, Tachyglossus aculeatus, Thylogale stigmatica, Thylogale thetis, Trichosurus caninus, Trichosurus vulpecula, Vombatus ursinus, Wallabia bicolor*
42*	Paluma Range	*Acrobates pygmaeus, Antechinus adustus, Antechinus flavipes, Dactylopsila trivirgata, Dasyurus hallucatus, Isoodon macrourus, Perameles nasuta, Petauroides volans, Petaurus breviceps, Petaurus gracilis, Pseudocheirus peregrinus, Pseudochirops archeri, Pseudomys delicatulus, Rattus fuscipes, Rattus leucopus, Rattus lutreolus, Tachyglossus aculeatus, Thylogale stigmatica, Uromys caudimaculatus*
43	Paroo Darling	*Antechinomys laniger, Bettongia lesueur, Leggadina forresti, Macropus fuliginosus, Macropus giganteus, Macropus robustus, Macropus rufus, Phascolarctos cinereus, Planigale gilesi, Planigale tenuirostris, Pseudomys hermannsburgensis, Sminthopsis crassicaudata, Sminthopsis macroura*

Site ID#	Site	Species List [a]
44	Torrington	*Acrobates pygmaeus, Antechinus flavipes, Macropus giganteus, Macropus robustus, Macropus rufogriseus, Petaurus breviceps, Phascogale tapoatafa, Rattus fuscipes, Tachyglossus aculeatus, Wallabia bicolor*
45	Tully Gorge	*Dasyurus hallucatus, Hydromys chrysogaster, Melomys burtoni, Perameles nasuta, Pseudochirops archeri, Rattus sordidus, Uromys caudimaculatus*
46	Undara Volcanic	*Aepyprymnus rufescens, Isoodon macrourus, Leggadina lakedownensis, Macropus antilopinus, Macropus giganteus, Macropus parryi, Macropus robustus, Petrogale mareeba, Pseudomys delicatulus, Rattus sordidus, Trichosurus vulpecula*
47*	Washpool	*Acrobates pygmaeus, Aepyprymnus rufescens, Antechinus flavipes, Antechinus stuartii, Antechinus swainsonii, Cercartetus nanus, Dasyurus hallucatus, Isoodon macrourus, Macropus giganteus, Macropus parma, Macropus parryi, Macropus robustus, Macropus rufogriseus, Perameles nasuta, Petauroides volans, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Petrogale penicillata, Phascogale tapoatafa, Phascolarctos cinereus, Potorous tridactylus, Pseudocheirus peregrinus, Pseudomys gracilicaudatus, Pseudomys novaehollandiae, Pseudomys oralis, Rattus fuscipes, Rattus lutreolus, Sminthopsis murina, Thylogale stigmatica, Thylogale thetis, Trichosurus vulpecula, Vombatus ursinus, Wallabia bicolor*
48	Welford	*Macropus giganteus, Macropus robustus, Macropus rufus, Pseudomys hermannsburgensis, Sminthopsis crassicaudata, Tachyglossus aculeatus, Zyzomys argurus*
49	White Mountains	*Lagorchestes conspicillatus, Petaurus breviceps, Planigale maculata, Pseudomys delicatulus, Pseudomys desertor, Pseudomys patrius, Zyzomys argurus*
50*	Wollemi	*Acrobates pygmaeus, Antechinus flavipes, Antechinus stuartii, Antechinus swainsonii, Cercartetus nanus, Dasyurus hallucatus, Hydromys chrysogaster, Isoodon obesulus, Macropus giganteus, Macropus parma, Macropus robustus, Macropus rufogriseus, Perameles nasuta, Petauroides volans, Petaurus australis, Petaurus breviceps, Petaurus norfolcensis, Petrogale penicillata, Phascogale tapoatafa, Phascolarctos cinereus, Planigale maculata, Pseudocheirus peregrinus, Pseudomys novaehollandiae, Rattus fuscipes, Rattus lutreolus, Sminthopsis murina, Tachyglossus aculeatus, Thylogale stigmatica, Trichosurus caninus, Trichosurus vulpecula, Wallabia bicolor*
51*	Wooroonooran	*Antechinus adustus, Antechinus flavipes, Antechinus godmani, Cercartetus caudatus, Dactylopsila trivirgata, Dasyurus hallucatus, Dendrolagus lumholtzi, Hemibelideus lemuroides, Hydromys chrysogaster, Hypsiprymnodon moschatus, Isoodon macrourus, Melomys burtoni, Melomys*

Site ID#	Site	Species List [a]
		cervinipes, Perameles nasuta, Pseudocheirus peregrinus, Pseudochirops archeri, Pseudochirulus herbertensis, Rattus fuscipes, Rattus leucopus, Rattus sordidus, Thylogale stigmatica, Trichosurus vulpecula, Uromys caudimaculatus, Wallabia bicolor

[a] Compiled from: (1) the NSW Office of Environment and Heritage's Atlas of NSW Wildlife (http://www.environment.nsw.gov.au/atlaspublicapp/UI_Modules/ATLAS_/AtlasSearch.aspx), which holds data from a number of custodians. Data obtained through the BioNet Atlas of NSW Wildlife using only detailed systematic fauna survey information from scientific surveys; (2) the Queensland Government Wildlife Onlife (WildNet; https://environment.ehp.qld.gov.au/report-request/species-list/) database of wildlife sightings from Queensland Government departments and external organizations. Only data from confirmed sightings was used; (3) the Atlas of Living Australia (http://biocache.ala.org.au/search#advanced) database using only georeferenced observation records.

Table A.3. Malagasy environmental matrix. Latitude and longitude are extracted for the protected area centroid. Year refers to the year the area began being protected (year gazetted unless otherwise indicated). Area is calculated from shapefiles of protected area boundaries where possible. Mean values reported for elevation, precipitation and temperature variables calculated across the entire protected area.

Site #	Site Name	Latitude (dd)	Longitude (dd)	Year [a]	Area (km^2) [b]	Elevation (m)	Annual Mean Precip. (mm)	Annual Mean Temp. (°C) [c]	Precip. Seasonality (cov)	Temp. Seasonality (SD*100)
1	Ambohijanajary	-18.60	45.63	1958	242.97	918.34	1597.60	22.17	102.18	1784.76
2	Ambohitantely	-18.08	47.16	1982	49.51	1448.92	1407.35	18.14	106.98	2164.57
3	Analamazaotra	-19.00	48.50	1970	8.90	986.70	1834.10	19.02	67.00	2580.10
4	Analavelona	-22.64	44.18	1989	330.65	912.28	742.76	21.23	106.17	2488.17
5	Andohahela: Parcel 1 Humid [d]	-24.70	46.73	1939	371.21	615.50	1104.59	21.40	58.68	2489.37
6	Andohahela: Parcel 1 Subhumid [d]	-24.68	46.74	1939	356.11	1165.78	1102.01	18.37	63.36	2348.07
7	Andohahela: Parcel 2	-24.89	46.57	1939	130.33	234.00	869.82	22.60	56.45	2698.82
8	Andringitra: Humid [d]	-22.23	46.90	1927	5.70	800.00	1218.63	20.24	87.00	2525.75
9	Andringitra: Subhumid [d]	-22.23	46.93	1927	304.31	1698.36	1254.46	15.81	90.19	2406.33
10	Anjanaharibe-Sud	-14.55	49.40	1958	183.50	1209.81	1676.15	18.98	74.56	2202.08
11	Anjozorobe	-18.47	47.95	2005	524.12	1248.11	1397.34	18.27	94.41	2466.73
12	Ankarafantsika	-16.23	46.90	1927	1351.22	164.13	1509.52	26.34	120.33	1412.86
13	Ankarana	-12.92	49.10	1956	254.36	193.30	1584.40	25.48	106.18	1216.82
14	Bemaraha	-18.65	44.75	1997	1562.24	339.00	1306.35	24.82	109.61	1844.34
15	Berenty Reserve	-24.83	46.33	1936	4.58	27.40	563.00	24.32	55.00	2974.40
16	Beza Mahafaly	-23.68	44.58	1978	4.54	162.33	630.50	25.07	100.50	3029.33
17	Forêt des Mikea	-22.30	43.47	2008 [1]	3217.51	54.54	513.54	24.42	115.06	2584.35
18	Isalo	-22.72	45.45	1962	865.79	837.24	782.08	21.95	104.84	2296.61
19	Kirindy CFPF	-20.05	44.68	1978	1068.16	54.25	924.85	25.90	125.81	2238.27
20	Kirindy-Mitea	-20.81	44.14	1997	1286.64	62.37	734.47	25.16	129.73	2514.35

Site #	Site Name	Latitude (dd)	Longitude (dd)	Year [a]	Area (km^2) [b]	Elevation (m)	Annual Mean Precip. (mm)	Annual Mean Temp. (°C) [c]	Precip. Seasonality (cov)	Temp. Seasonality (SD*100)
21	Manongarivo	-13.98	48.38	1956	417.03	1145.00	1514.67	21.08	103.67	1621.17
22	Mantadia	-18.95	48.60	1989	154.94	1028.56	1825.64	19.17	68.89	2634.47
23	Marojejy: Humid [d]	-14.45	49.81	1952	233.05	587.32	1783.30	21.79	60.28	2037.22
24	Marojejy: Subhumid [d]	-14.45	49.68	1952	368.11	1100.51	1661.25	19.37	68.12	2127.32
25	Masoala	-15.53	50.05	1997	2103.86	463.89	2422.87	21.93	42.39	2056.22
26	Montagne d'Ambre	-12.53	49.17	1958	227.52	920.86	1379.20	21.04	97.42	1377.47
27	Namoroka	-16.47	45.36	1927	221.33	141.66	1352.35	25.90	122.06	1442.76
28	Ranomafana	-21.27	47.47	1991	405.61	1101.30	1647.02	18.18	77.11	2564.14
29	Tsaratanana	-14.15	48.96	1927	493.99	1287.67	1491.69	19.21	96.39	1829.92
30	Tsimanampesotse	-24.12	43.80	1927	458.35	86.55	441.25	24.30	91.67	2694.08
31	Tsinjoarivo [e]	-19.70	47.80	2007 [2]	n.c. [2]	1515.41	1480.11	16.70	79.17	2595.30
32	Verzanantsoro	-16.25	49.67	1989 [3]	229.14	384.42	2429.48	22.34	47.38	2080.88
33	Zahamena	-17.60	48.88	1927	415.35	1157.35	1247.83	18.75	87.13	2401.32
34	Zombitse-Vohibasia	-22.62	44.82	1997	172.43	687.84	740.50	22.66	105.05	2637.79

[a] Year the designated area was gazetted or protection began. Citations unleass otherwise indicated: IUCN and UNEP 2014 (data provided by ANGAP via Conservation International)

[b] Calculated from the shapefiles of park boundaries projected as UTM Zone 38S WGS1984. Citations unless otherwise indicated: Gerber 2010; IUCN and UNEP 2014

[c] Temperature in the Bioclim dataset is provideded as °C*10, it is presented here without this transformation.

[d] cf. Muldoon and Goodman (2010) classification: Humid forest (0-800m elevation), Subhumid forest (800-1600m elevation); area for subhumid forest calculated as portion of protected area above 800m elevation.

[e] The location reported here is for Tsinjoarivo Classified Forest (Vatateza camp region), the largest piece of continuous primary forest (Irwin et al. 2010).

[l] in November 2008, the regional committee for the creation of the National Park approved its boundaries (Blanc-Pamard 2009).

[2] area is a classified forest, however not officially protected by the Malagasy government. Sadabe (Irwin 2009), an NGO, started for the protection of the region and the site has been recommended as a new protected area (Andriaholinirina et al. 2014). The area of the site was not calculated (n.c.) from a shape file because it has no clear boundaries of protection (M. Irwin 2014, pers. comm., 11 November). The environmental variable means were calculated from a 10km buffer region around the site coordinates.
[3] declared as classified forest in 1965; law establishing the 'Réserve de la biosphère â Mananara-Nord', within which Verzanatsoro exists, was passed in 1989. A biosphere reserve nomination, submitted by the Direction des Eaux et Forêts, was accepted in 1990 (World Conservation Monitoring Centre 1990)

Table A.4. Australian environmental matrix**.** Latitude and longitude are extracted for the protected area centroid projected in UTM. Year refers to the year the area began being protected (year gazetted unless otherwise indicated). Area is calculated from shapefiles of protected area boundaries. Mean values reported for elevation, precipitation and temperature variables calculated across the entire protected area. * indicate Australian sites with ≥ 5 arboreal mammal species.

Site #	Site Name	Latitude (dd)	Longitude (dd)	Year [a]	Area (km^2)[b]	Elevation (m)	Annual Mean Precip. (mm)	Annual Mean Temp. (°C) [c]	Precip. Seasonality (cov)	Temp. Seasonality (SD*100)
1*	Abercrombie River	-34.11	149.70	1995	188.90	828.41	851.94	11.87	11.19	4835.62
2*	Arakoon	-30.89	153.07	1974	1.46	13.67	1450.85	18.70	36.29	3442.11
3*	Arakwal	-28.66	153.62	2001	1.86	12.33	1815.00	19.87	31.00	3256.00
4*	Bangadilly	-34.45	150.19	2001	21.35	661.34	846.38	12.91	20.38	4522.09
5	Blackbraes	-19.58	144.02	1900	296.55	911.21	732.77	21.25	102.72	4039.08
6	Bladensburg	-22.64	143.07	1900	842.60	244.35	424.96	23.64	78.73	5346.15
7*	Blue Mountains	-34.01	150.37	1967	2677.86	615.32	1087.04	13.52	28.97	4557.67
8	Boodjamulla (Lawn Hill)	-18.64	138.28	1900	2833.01	205.92	540.72	25.53	107.69	4281.60
9*	Border Ranges	-28.40	152.84	1979	316.49	569.29	1563.86	16.76	43.66	3739.62
10	Cape Melville	-14.53	144.61	1900	1717.72	84.52	1305.37	25.61	105.81	1941.10
11*	Carnarvon	-25.04	148.25	1900	3013.21	699.00	689.73	18.73	49.85	5271.37
12*	Carrai	-30.90	152.24	1999	113.33	845.30	1204.76	13.88	38.56	4220.43
13*	Chiltern Mt.Pilot	-36.25	146.72	1980	215.93	355.20	858.38	13.45	29.69	5273.17
14	Currawinya	-28.84	144.33	1900	1542.15	137.88	319.36	20.66	38.57	6098.72
15*	Daintree	-16.27	145.18	1900	769.15	554.51	1768.11	22.79	89.98	2248.67
16	Diamantina	-23.82	141.46	1900	5108.96	121.11	255.19	23.92	71.62	5791.44
17*	Dunggir	-30.69	152.68	1997	25.83	425.79	1597.52	16.29	44.15	3928.45
18*	Eungella	-21.09	148.57	1900	596.22	649.97	1174.84	19.92	75.88	3611.06
19	Expedition (Limited Depth)	-25.58	149.01	1900	1096.22	498.88	681.61	19.23	46.13	5150.99
20	Forest Den	-22.12	145.22	1900	59.14	244.40	504.88	23.60	73.51	4740.92

Site #	Site Name	Latitude (dd)	Longitude (dd)	Year [a]	Area (km^2)[b]	Elevation (m)	Annual Mean Precip. (mm)	Annual Mean Temp. (°C) [c]	Precip. Seasonality (cov)	Temp. Seasonality (SD*100)
21*	Gibraltar Range	-29.51	152.36	1967	254.00	839.84	1250.19	14.76	43.44	4236.28
22*	Girringun	-18.37	145.70	1900	2041.63	465.22	1503.58	22.05	86.07	3056.85
23*	Great Sandy	-25.40	153.15	1900	2238.89	70.10	1379.50	21.37	38.37	3056.62
24*	Gumbaynggirr	-30.54	152.56	2007	49.08	453.21	1543.47	16.29	45.62	4011.48
25	Gundabooka	-30.58	145.75	1996	641.12	138.18	355.36	19.77	28.00	5852.41
26*	Guy Fawkes River	-30.04	152.20	1972	1052.31	767.69	1152.98	14.86	45.65	4335.82
27*	Herberton Range	-17.40	145.46	1900	63.53	1018.20	1437.80	19.39	78.98	2814.49
28	Idalia	-24.95	144.68	1900	1409.10	373.76	465.06	21.65	53.19	5715.35
29	Jardine River	-11.30	142.61	1900	2344.57	62.39	1751.00	26.23	108.03	1144.76
30	Kakadu	-13.49	132.44	1979	19086.28	105.25	1383.18	27.37	106.08	2135.58
31	Kinchega	-32.51	142.30	1967	445.59	64.19	257.31	18.39	17.56	5498.27
32*	Kirrama	-18.17	145.71	1900	172.19	727.81	1519.20	20.70	80.72	3027.02
33*	Lamington	-28.28	153.12	1900	206.29	702.55	1737.76	16.21	42.04	3530.53
34	Mallee Cliffs	-34.20	142.62	1977	580.90	75.50	317.25	16.99	13.16	5230.17
35*	Mebbin	-28.50	153.16	1999	37.76	359.24	1663.60	17.98	45.26	3643.36
36*	Mitchell Plateau	-37.31	142.57	1992	69.14	478.29	680.56	12.80	28.00	3975.06
37*	Morton	-34.93	150.23	1967	1973.99	471.55	1074.47	13.91	20.72	4168.58
38	Mungo	-33.43	143.00	1979	1121.41	77.86	301.61	17.62	12.73	5436.04
39*	Myall Lakes	-32.45	152.36	1972	480.19	63.31	1335.04	17.72	27.92	3652.83
40*	New England	-30.68	152.47	1967	696.18	603.49	1408.45	15.44	44.36	4119.69
41*	Oxley Wild Rivers	-31.12	152.09	1986	1420.07	677.63	1011.95	14.75	40.84	4412.51
42*	Paluma Range	-19.10	146.30	1900	706.13	565.18	1012.27	21.52	86.18	3247.16
43	Paroo-Darling	-30.81	143.54	2000	1760.57	96.76	273.90	19.48	25.03	5959.62
44	Torrington	-29.23	151.58	1996	302.72	878.05	818.17	14.65	32.23	4876.45

Site #	Site Name	Latitude (dd)	Longitude (dd)	Year [a]	Area (km^2)[b]	Elevation (m)	Annual Mean Precip. (mm)	Annual Mean Temp. (°C) [c]	Precip. Seasonality (cov)	Temp. Seasonality (SD*100)
45	Tully Gorge	-17.88	145.81	1900	600.05	431.87	2342.76	22.04	77.93	2851.42
46	Undara Volcanic	-18.31	144.61	1900	666.57	767.78	720.27	21.69	107.76	3362.69
47*	Washpool	-29.42	152.27	1983	674.40	858.57	1161.57	14.73	41.42	4281.14
48	Welford	-25.08	143.37	1900	1234.37	184.90	316.29	22.83	56.42	5936.27
49	White Mountains	-20.51	144.96	1900	1077.83	587.20	628.00	22.44	86.43	4233.65
50*	Wollemi	-33.42	150.55	1979	5012.93	553.82	880.29	14.60	31.52	4772.27
51*	Wooroonooran	-17.36	145.81	1900	1136.92	514.91	2879.30	21.62	73.40	2698.92

[a] Year the designated area was gazetted or protection began (CAPAD 2008).
[b] Calculated from the shapefiles of park boundaries (CAPAD 2008) projected as GDA 1994 Geoscience Australia Lambert.
[c] Temperature in the Bioclim dataset is provideded as °C*10, it is presented here without this transformation.

Table A.5. Description of mammal traits related to resource use used to calculate the functional diversity of each community type. Data from field studies where possible, unless the only data available was from captivity. Trait values are provided in Table A.6 and A.9.

Traits	Classification of traits and trait types	Data type
Body mass		
combined mass of adult males and females	Body mass of adult individuals. Median value of referenced values used.	Continuous
Substrate type		Categorical
terrestrial; arboreal; both terrestrial and arboreal	Substrate it spends the majority of its daily activity budget on (not including sleep), i.e rarely found in alternate subtsrate type by researchers. Both terrestrial and arboreal species are found being active in both substrate types.	
Feeding guild	Consumes mostly (40% or more where calculated) that food category during a year.	Categorical
folivore	Consumes predominantly leaves (species is physiologically adapted to consuming leaves); this category includes consumption of forbs.	
herbivore	Consumes predominantly nonleaf material (e.g., shrubs, stems, grasses etc.).	
frugivore	Consumes predominantly fruits; this category also flower consumption.	
gumnivore	Consumes predominantly gum; this category also include nectarivores.	
granivore	Consumes predominantly seeds.	
insectivore	Consumes predominantly invertebrate prey (e.g., insects, earthworms)	
carnivore	Consumes primarily vertebrate prey.	
omnivore	Consumes almost equal proportions of both animal and plant matter.	
Trophic level	Determined based on feeding guild.	Categorical
primary consumer	Includes folivores, herbivores, frugivores, gumnivores, and granivores.	
secondary consumer	Includes insectivores; omnivores if they do not eat vertebrate prey.	
tertiary consumer	Includes carnivores; omnivores if they eat vertebrate prey.	

Traits	Classification of traits and trait types	Data type
Locomotion	Location of and type of locomotion habitually used (cf. Baudinette 1994; Fleagle 1999; Schmidt 2010; Szalay 1994).	Categorical
arboreal quadruped	Individuals use four limbs in locomotion on arboreal substrates (Fleagle 1999). Counted as an arboreal quadruped if individuals forage and nest in the trees, are rarely to never found on the ground, or have specific anatomical adaptations to arboreal quadrupedalism.	
gliding arboreal quadruped	Individuals with adapted membranes for gliding flight.	
terrestrial/arboreal quadruped	Individuals forage and nest both in the trees and on the ground, or individuals do not have specific anatomical adaptations to terrestrial or arboreal locomotion. Includes terrestrial species with scansorial adaptations, where scansoriality is used for foraging.	
terrestrial quadruped	Individuals use four limbs in locomotion on terrestrial substrates (Fleagle 1999). Counted as a terrestrial quadruped if individuals forage and nest on the ground, are most often found on the ground, or have specific anatomical adaptations to terrestrial quadrupedalism.	
vertical clinger and leaper	Arboreal species that leap from a vertical clinging position between discontinuous supports.	
hind-limb locomotion	Individuals move bipedally by hopping (also refererred to as bipedal hopping).	
semi-aquatic	Individuals commonly forage and travel in the water.	
fossorial	Individuals burrow into the ground for foraging or nesting.	
Activity period		Categorical
diurnal; nocturnal; cathemeral	Time of day species spends most of its time active in. Cathemeral species are active throughout the day and night (Tattersal 1987).	
Habitat specificity		Discrete
number of ecoregions occupied	Determined from number of ecoregions the species is part of an assemblage list.	
Torpor		Categorical
Yes; No	'Yes' if species has a regulated period of lower metabolic rate, which results in body temperature approaching ambient temperature (Geiser 2004). Species reported to aestivate or hibernate are also included in this category (i.e. no differentiation based on time in this state is reported, Ruf et al. 2012).	

Table A.6. Malagasy nonvolant mammal species trait data included in analyses. Trait details provided in Table A.5. Publication cut-off date for included sources of information was January 2013.*

Family	Species	Body mass (g) [a]	Arb. or Terr. [b]	Feeding guild [c]	Trophic level [d]	Loco. [e]	Activity Period [f]	Habitat Specificity	Torpor [g]
Order Afrosoricida									
Tenrecidae	*Echinops telfairi*	140.6	Both	IN	2	Q	Noct.	4	Yes
Tenrecidae	*Geogale aurita*	6	Terr.	IN	2	TQ	Noct.	3	Yes
Tenrecidae	*Hemicentetes nigriceps*	160	Terr.	IN	2	TQ	Noct.	1	Yes
Tenrecidae	*Hemicentetes semispinosus*	220	Terr.	IN	2	TQ	Noct.	2	Yes
Tenrecidae	*Limnogale mergulus*	79	Terr.	CA	3	SA	Noct.	1	No
Tenrecidae	*Microgale brevicaudata*	11	Terr.	IN	2	TQ	Noct.	4	No
Tenrecidae	*Microgale cowani*	13.3	Terr.	IN	2	TQ	Noct.	2	dd
Tenrecidae	*Microgale dobsoni*	25.5	Terr.	IN	2	Q	Noct.	2	Yes
Tenrecidae	*Microgale drouhardi*	14.8	Terr.	IN	2	TQ	Noct.	2	dd
Tenrecidae	*Microgale fotsifotsy*	7.7	Terr.	IN	2	Q	Noct.	1	dd
Tenrecidae	*Microgale gracilis*	23.2	Terr.	IN	2	F	Noct.	2	dd
Tenrecidae	*Microgale grandidieri*	8.9	Terr.	IN	2	TQ	Noct.	1	dd
Tenrecidae	*Microgale gymnorhyncha*	15.8	Terr.	IN	2	F	Noct.	1	dd
Tenrecidae	*Microgale jenkinsae*	5.3	Terr.	IN	2	TQ	Noct.	1	dd
Tenrecidae	*Microgale jobihely*	9	Terr.	IN	2	TQ	Noct.	1	dd
Tenrecidae	*Microgale longicaudata*	7	Both	IN	2	Q	Noct.	3	dd
Tenrecidae	*Microgale majori*	7	Both	IN	2	Q	Noct.	4	dd
Tenrecidae	*Microgale monticola*	15.5	Terr.	IN	2	TQ	Noct.	1	dd
Tenrecidae	*Microgale nasoloi*	14	Terr.	IN	2	TQ	Noct.	2	dd
Tenrecidae	*Microgale parvula*	3.7	Terr.	IN	2	TQ	Noct.	1	dd
Tenrecidae	*Microgale principula*	10.7	Terr.	IN	2	Q	Noct.	2	dd
Tenrecidae	*Microgale pusilla*	3.6	Terr.	IN	2	TQ	Noct.	1	dd
Tenrecidae	*Microgale soricoides*	18.1	Both	IN	2	Q	Noct.	2	dd
Tenrecidae	*Microgale taiva*	12.4	Terr.	IN	2	TQ	Noct.	2	dd
Tenrecidae	*Microgale talazaci*	36	Terr.	IN	2	TQ	Noct.	1	Yes
Tenrecidae	*Microgale thomasi*	22.4	Terr.	IN	2	TQ	Noct.	2	dd
Tenrecidae	*Oryzorictes hova*	40	Terr.	IN	2	F	Noct.	2	dd
Tenrecidae	*Setifer setosus*	282	Terr.	OM	2	Q	Noct.	5	Yes
Tenrecidae	*Tenrec ecaudatus*	832	Terr.	OM	2	TQ	Noct.	5	Yes

Family	Species	Body mass (g) [a]	Arb. or Terr. [b]	Feeding guild [c]	Trophic level [d]	Loco. [e]	Activity Period [f]	Habitat Specificity	Torpor [g]
Order Carnivora									
Eupleridae	*Cryptoprocta ferox*	6100	Both	CA	3	Q	Cath.	5	No
Eupleridae	*Eupleres goudotii*	4500	Terr.	IN [1]	2	TQ	Noct.	3	No
Eupleridae	*Fossa fossana*	1700	Terr.	CA	3	TQ	Noct.	2	No
Eupleridae	*Galidia elegans*	720	Terr.	CA	3	Q	Diurn.	3	No
Eupleridae	*Galidictis fasciata*	745	Terr.	CA	3	TQ	Noct.	2	No
Eupleridae	*Galidictis grandidieri*	1470	Terr.	CA	3	TQ	Noct.	1	No
Eupleridae	*Mungotictis decemlineata*	550	Both	IN [2]	2	Q	Diurn.	3	dd
Eupleridae	*Salanoia concolor*	780	Both	CA	3	Q	Diurn.	1	No
Order Primates									
Cheirogaleidae	*Allocebus trichotis*	85	Arb.	IN	2	AQ	Noct.	2	Yes
Cheirogaleidae	*Cheirogaleus crossleyi*	119	Arb.	OM	2	AQ	Noct.	2	Yes
Cheirogaleidae	*Cheirogaleus major*	443	Arb.	OM	2	AQ	Noct.	2	Yes
Cheirogaleidae	*Cheirogaleus medius*	119	Arb.	OM	2	AQ	Noct.	4	Yes
Cheirogaleidae	*Microcebus arnholdi*	31	Arb.	OM	2	AQ	Noct.	1	Yes
Cheirogaleidae	*Microcebus berthae*	63	Arb.	OM	2	AQ	Noct.	1	Yes
Cheirogaleidae	*Microcebus griseorufus*	48	Arb.	OM	2	AQ	Noct.	1	Yes
Cheirogaleidae	*Microcebus lehilahytsara*	61	Arb.	OM	2	AQ	Noct.	1	dd
Cheirogaleidae	*Microcebus mittermeieri*	42	Arb.	OM	2	AQ	Noct.	2	dd
Cheirogaleidae	*Microcebus murinus*	62	Arb.	OM	2	AQ	Noct.	4	Yes
Cheirogaleidae	*Microcebus myoxinus*	49	Arb.	OM	2	AQ	Noct.	1	Yes
Cheirogaleidae	*Microcebus ravelobensis*	72	Arb.	OM	2	AQ	Noct.	1	Yes
Cheirogaleidae	*Microcebus rufus*	42	Arb.	OM	2	AQ	Noct.	2	Yes
Cheirogaleidae	*Microcebus sambiranensis*	44	Arb.	OM	2	AQ	Noct.	1	dd
Cheirogaleidae	*Microcebus simmonsi*	42	Arb.	OM	2	AQ	Noct.	1	dd
Cheirogaleidae	*Microcebus tavaratra*	61	Arb.	OM	2	AQ	Noct.	1	dd
Cheirogaleidae	*Mirza coquereli*	294	Arb.	OM	2	AQ	Noct.	3	No
Cheirogaleidae	*Phaner electromontis*	500	Arb.	GU	1	AQ	Noct.	3	dd
Cheirogaleidae	*Phaner furcifer*	500	Arb.	GU	1	AQ	Noct.	1	dd
Cheirogaleidae	*Phaner pallescens*	350	Arb.	GU	1	AQ	Noct.	4	No
Cheirogaleidae	*Phaner parienti*	350	Arb.	GU	1	AQ	Noct.	1	dd
Daubentoniidae	*Daubentonia madagascariensis*	2550	Arb.	OM	2	AQ	Noct.	3	No
Indriidae	*Avahi cleesei*	830	Arb.	FO	1	VCL	Noct.	1	No
Indriidae	*Avahi laniger*	1207	Arb.	FO	1	VCL	Noct.	2	No

Family	Species	Body mass (g) [a]	Arb. or Terr. [b]	Feeding guild [c]	Trophic level [d]	Loco. [e]	Activity Period [f]	Habitat Specificity	Torpor [g]
Indriidae	*Avahi meridionalis*	1207	Arb.	FO	1	VCL	Noct.	2	No
Indriidae	*Avahi mooreorum*	1207	Arb.	FO	1	VCL	Noct.	1	No
Indriidae	*Avahi occidentalis*	816	Arb.	FO	1	VCL	Noct.	1	No
Indriidae	*Avahi peyrierasi*	1007	Arb.	FO	1	VCL	Noct.	1	No
Indriidae	*Avahi unicolor*	850	Arb.	FO	1	VCL	Noct.	1	No
Indriidae	*Indri indri*	6480	Arb.	FO	1	VCL	Diurn.	2	No
Indriidae	*Propithecus candidus*	5000	Arb.	FO	1	VCL	Diurn.	1	No
Indriidae	*Propithecus coquereli*	3760	Arb.	FO	1	VCL	Diurn.	1	No
Indriidae	*Propithecus deckenii*	3500	Arb.	FO	1	VCL	Diurn.	1	No
Indriidae	*Propithecus diadema*	6000	Arb.	FO	1	VCL	Diurn.	2	No
Indriidae	*Propithecus edwardsi*	5895	Arb.	FO	1	VCL	Diurn.	2	No
Indriidae	*Propithecus perrieri*	5000	Arb.	FO	1	VCL	Diurn.	1	No
Indriidae	*Propithecus verreauxi*	3525	Arb.	FO	1	VCL	Diurn.	2	No
Lemuridae	*Eulemur albifrons*	2550	Arb.	FR	1	AQ	Cath.	2	No
Lemuridae	*Eulemur cinereiceps*	2000	Arb.	FR	1	AQ	Cath.	2	No
Lemuridae	*Eulemur collaris*	2500	Arb.	FR	1	AQ	Cath.	2	No
Lemuridae	*Eulemur coronatus*	1687	Arb.	FR	1	AQ	Cath.	2	No
Lemuridae	*Eulemur fulvus*	2600	Arb.	FR	1	AQ	Cath.	3	No
Lemuridae	*Eulemur macaco*	2552	Arb.	FR	1	AQ	Cath.	1	No
Lemuridae	*Eulemur mongoz*	1658	Arb.	FR	1	AQ	Cath.	1	No
Lemuridae	*Eulemur rubriventer*	1960	Arb.	FR	1	AQ	Cath.	2	No
Lemuridae	*Eulemur rufifrons*	1820	Arb.[3]	FR	1	AQ	Cath.	4	No
Lemuridae	*Eulemur rufus*	2550	Arb.	FR	1	AQ	Cath.	4	No
Lemuridae	*Eulemur sanfordi*	2300	Arb.	FR	1	AQ	Cath.	2	No
Lemuridae	*Hapalemur aureus*	1548	Arb.	FO [4]	1	VCL	Diurn.	2	No
Lemuridae	*Hapalemur griseus*	700	Arb.	FO [4]	1	VCL	Diurn.	1	No
Lemuridae	*Hapalemur meridionalis*	700	Arb.	FO [4]	1	VCL	Diurn.	2	No
Lemuridae	*Hapalemur occidentalis*	700	Arb.	FO [4]	1	AQ	Noct.	2	No
Lemuridae	*Lemur catta*	2678	Both	FR	1	Q	Diurn. [5]	4	No
Lemuridae	*Prolemur simus*	2450	Arb.	FO [4]	1	VCL	Cath.	1	No
Lemuridae	*Varecia variegata*	3548	Arb.	FR	1	AQ	Diurn.	1	No
Lepilemuridae	*Lepilemur ankaranensis*	700	Arb.	FO	1	VCL	Noct.	1	No
Lepilemuridae	*Lepilemur dorsalis*	500	Arb.	FO	1	VCL	Noct.	1	No
Lepilemuridae	*Lepilemur edwardsi*	980	Arb.	FO	1	VCL	Noct.	1	No
Lepilemuridae	*Lepilemur fleuretae*	980	Arb.	FO	1	VCL	Noct.	1	No
Lepilemuridae	*Lepilemur hollandorum*	800	Arb.	FO	1	VCL	Noct.	1	No

Family	Species	Body mass (g) [a]	Arb. or Terr. [b]	Feeding guild [c]	Trophic level [d]	Loco. [e]	Activity Period [f]	Habitat Specificity	Torpor [g]
Lepilemuridae	*Lepilemur hubbardi*	990	Arb.	FO	1	VCL	Noct.	1	No
Lepilemuridae	*Lepilemur leucopus*	544	Arb.	FO	1	VCL	Noct.	1	No
Lepilemuridae	*Lepilemur microdon*	800	Arb.	FO	1	VCL	Noct.	2	No
Lepilemuridae	*Lepilemur mustelinus*	594	Arb.	FO	1	VCL	Noct.	2	No
Lepilemuridae	*Lepilemur petteri*	630	Arb.	FO	1	VCL	Noct.	1	No
Lepilemuridae	*Lepilemur randrianasoloi*	920	Arb.	FO	1	VCL	Noct.	1	No
Lepilemuridae	*Lepilemur ruficaudatus*	842	Arb.	FO	1	VCL	Noct.	4	No
Lepilemuridae	*Lepilemur scottorum*	594	Arb.	FO	1	VCL	Noct.	1	No
Lepilemuridae	*Lepilemur seali*	594	Arb.	FO	1	VCL	Noct.	1	No
Lepilemuridae	*Lepilemur septentrionalis*	700	Arb.	FO	1	VCL	Noct.	1	No
Order Rodentia									
Nesomyidae	*Brachytarsomys albicauda*	223	Arb.	FR	1	AQ	Noct.	2	dd
Nesomyidae	*Brachytarsomys villosa*	293	Arb.	FR	1	AQ	Noct.	1	dd
Nesomyidae	*Brachyuromys betsileoensis*	90.9	Terr.	HE	1	TQ	Cath.	1	dd
Nesomyidae	*Brachyuromys ramirohitra*	128	Terr.	HE	1	TQ	Cath.	1	dd
Nesomyidae	*Eliurus antsingy*	90	Arb.	GR	1	AQ	Noct.	1	dd
Nesomyidae	*Eliurus carletoni*	94.8	Arb.	GR	1	AQ	Noct.	1	dd
Nesomyidae	*Eliurus danieli*	95.5	Terr.	GR	1	TQ	Noct.	1	dd
Nesomyidae	*Eliurus grandidieri*	50.6	Terr.	GR	1	TQ	Noct.	2	dd
Nesomyidae	*Eliurus majori*	97.2	Arb.	GR	1	AQ	Noct.	2	dd
Nesomyidae	*Eliurus minor*	35.1	Arb.	GR	1	AQ	Noct.	3	dd
Nesomyidae	*Eliurus myoxinus*	65.8	Arb.	GR	1	AQ	Noct.	4	dd
Nesomyidae	*Eliurus tanala*	81.7	Arb.	GR	1	Q	Noct.	3	dd
Nesomyidae	*Eliurus webbi*	70.1	Terr.	GR	1	Q	Noct.	2	dd
Nesomyidae	*Gymnuromys roberti*	127	Terr.	GR	1	TQ	Noct.	2	dd
Nesomyidae	*Hypogeomys antimena*	1110	Terr.	GR	1	TQ	Noct.	1	No
Nesomyidae	*Macrotarsomys bastardi*	24.5	Terr.	GR	1	TQ	Noct.	3	dd
Nesomyidae	*Macrotarsomys ingens*	24.5	Arb.	GR	1	Q	Noct.	1	dd
Nesomyidae	*Macrotarsomys petteri*	105	Terr.	GR	1	TQ	Noct.	1	dd
Nesomyidae	*Monticolomys koopmani*	22.6	Terr.	GR	1	Q	Noct.	1	dd
Nesomyidae	*Nesomys audeberti*	211	Terr.	GR	1	TQ	Diurn.	2	dd
Nesomyidae	*Nesomys lambertoni*	233	Terr.	GR	1	TQ	Diurn.	1	dd
Nesomyidae	*Nesomys rufus*	159	Terr.	GR	1	TQ	Diurn.	1	dd
Nesomyidae	*Voalavo antsahabensis*	22	Both	FR	1	Q	Noct.	1	dd

Family	Species	Body mass (g) [a]	Arb. or Terr. [b]	Feeding guild [c]	Trophic level [d]	Loco. [e]	Activity Period [f]	Habitat Specificity	Torpor [g]
Nesomyidae	*Voalavo gymnocaudus*	22.5	Both	FR	1	Q	Noct.	2	No

Abbreviations: Terr., terrestrial; Arb., arboreal; Both, terrestrial and arboreal; CA, carnivore; FO, folivore; GR, granivore; GU, gumnivore; HE; herbivore; IN, insectivore; OM, omnivore; Loco., locomotion; AQ, arboreal quadruped; F, fossorial; HL; hindlimb locomotion; Q, arboreal and terrestrial quadruped; SA, semi-aquatic; TQ, terrestrial quadruped; VCL, vertical clinger and leaper; Diurn., diurnal; Noct., nocturnal; Cath., cathemeral; spec., specificity; dd, data deficient.

[*] Traits from the most recent studies prior to the cut-off date are provided. Published data compilations were used where possible and supplementary references are provided for species not present in large published datasets. Literature searches were completed in Google Scholar and Web of Science.

[a] *Afrosoricida*: Goodman and Benstead 2003; *Carnivora*: Dollar 2006; Goodman and Benstead 2003; Jones et al. 2009; *Primates*: Smith and Jungers 1997; Rasoloarison et al. 2000; Goodman et al. 2003a; Jones et al. 2009; Kappeler et al. 2005; Thalmann and Geissmann 2005; Andriaholinirina et al. 2006; Louis et al. 2006; Craul et al. 2007; Andriantompohavana et al. 2007; Oliveri et al. 2007; Lei et al. 2008; Louis et al. 2008; Radespiel et al. 2008; Ramaromilanto et al. 2009; *Rodentia*: Goodman and Benstead 2003; Carleton and Goodman 2007; Goodman et al. 2005; Jones et al. 2009

[b] *Afrosoricida*: Andrianjakarivelo et al. 2005; Dammhahn et al. 2013; Jenkins 2003; Garbutt 2007; Goodman 2003a; Goodman et al. 2006; Goodman and Soarimalala 2004; Rasolonandrasana and Goodman 2006; Salton and Szalay 2004; Salton and Sargus 2008; Stephenson 2003a; *Carnivora*: Albignac 1972; Albignac 1984; Barden et al. 1991; Britt and Virkaitis 2003; Dollar 1999, Garbutt 2007; Goodman 2003b; Goodman et al. 2003b; Goodman and Benstead 2003; Hawkins 2003; Nowak 1999; Razafimanantsoa 2003; *Primates*: Balko 1996; Fleagle 1999; Freed 1996; Ganzhorn 1988; Garbutt 2007; Jolly 1966; Kappeler 2003; Martin 1973; Meier and Albignac 1989; Meier and Albignac 1991; Meldrum et al. 1997; cf. Muldoon and Goodman 2010 (AQ and VCL = arboreal; TQ = terrestrial); Muller and Thalmann 2002; Overdorff 1996; Petter 1962; Sussman 1974; Tattersall 1982; Wright and Martin 1995; Vasey 2000; Vasey 2002; *Rodentia*: Andrianjakarivelo et al. 2005; Carleton 1994; Carleton 2003; Carleton and Goodman 1996, 2000, 2003; cf. Carleton and Goodman 2007; Goodman and Benstead 2003; Goodman and Carleton 1996; Goodman and Soarimalala 2005; Goodman et al. 1999; Goodman et al. 2003a; Laakkonen et al. 2003; Ramanamanjato and Ganzhorn 2001; Rasolonandrasana and Goodman 2006; Ryan 2003; Ryan et al. 1993; Sommer 2003

[c] *Afrosoricida*: Dammhahn et al. 2013; Garbutt 2007; Goodman et al. 2003a; Muldoon and Goodman 2010; Stephenson 1994a; Vololomboahangy and Goodman 2008; *Carnivora*: Dollar 2006; Garbutt 2007; Goodman et al. 2003a, b; Hawkins and Racey 2008; Jones et al. 2009; Mahazotahy et al. 2006; *Primates*: Biebouw 2009; Birkinshaw and Colquhoun 2003; Garbutt 2007; Goodman et al. 2003a; Jones et al. 2009; Radespiel et al. 2006; Simmen et al. 2003; Vasey 2000; Viguer 2004; Yamashita 2002; *Rodentia*: Goodman et al. 2003a; Garbutt 2007; Jones et al. 2009; Miljutin and Lehtonen 2008; Muldoon and Goodman 2010

[d] 1 = primary consumer; 2 =secondary consumer; 3= tertiary consumer

[e] *Afrosoricida*: Goodman and Benstead 2003; Muldoon and Goodman 2010; *Carnivora*: Dollar 2006; Goodman et al. 2003b; Goodman and Benstead 2003; Hawkins and Racey 2008; Mahazotahy et al. 2006; *Primates*: Fleagle 1999; *Rodentia*: Goodman and Benstead 2003; Muldoon and Goodman 2010

[f] Garbutt 2007; Goodman *et al*. 2003a; Jones et al. 2009; *Carnivora*: Bennie et al. 2014; Gerber et al. 2012; *Afrosoricida*: Bennie et al. 2014; Goodman et al. 2003a; *Primates*: Donati and Borgognini-Tarli 2006; Colquhoun 2007; Mutschler and Tan 2003; Ralainasolo et al. 2008; Tattersall 1987; *Rodentia*: Bennie et al. 2014;

[g] *Afrosoricida*: Benstead et al. 2001; McNab 2008; Nicoll 2003; Nowak 1999; Stephenson 1991; 1994b; 2003b; Wein 2010; *Carnivora*: Garbutt 2007; Nowak 1999; *Primates*: Biebouw 2009; Blanco and Rahalinarivo 2010; Dausmann 2004; Genin and Peret 2003; Hladik et al. 1980; Horvarth and Willard 2007; Jürges et al. 2013; Kappeler 2003; Kobbe et al. 2011; Morland 1993; Randrianambinina et al. 2003; Schmid 1999, 2000; Schmid et al. 2000; Schülke and Ostner 2007; Wright and Martin 1995; *Rodentia*: Garbutt 2007; Nowak 1999

[1] specializes on earthworms and insects (Albignac 1974; Hawkins 1994)

[2] primarily insectivorous, although diet is supplemented with small vertebrate prey items (Rabeantoandro 1997)

[3] based on ecological similarity to *Eulemur fulvus* cf. Mittermeier et al. 2008

[4] categorized as a folivore because of specialized adaptations to consuming bamboo, although not only the leaves are consumed (Grassi 2006; Tan 1999; Wright et al. 2008)

[5] not considered cathmeral in this study as evidence for cathemerality is preliminary (Parga 2011) and/or published after cuttoff date (Donati et al. 2013; LaFleur et al. 2014).

Table A.7. Malagasy primate species according to Mittermeier et al.'s 2010 phylogeny (to the species level) and taxonomic equivalences in the Genbank taxonomy that accompanies the 10K Trees Project primate consensus tree (Arnold *et al*. 2010). The Genbank taxonomy was only used for calculating phylogenetic measures of diversity. Only species for which a change in species name or which was absent from the primate consensus tree are included below.

Species	**Name in 10K Tree**	**Species**	**Name in 10K Tree**
Avahi meridionalis	Not present	*Lepilemur fleuretae*	Not present
Avahi mooreorum	Not present	*Lepilemur hollandorum*	Not present
Avahi peyrierasi	Not present	*Lepilemur hubbardi*	*Lepilemur hubbardorum*
Eulemur albifrons	*Eulemur fulvus albifrons*	*Lepilemur petteri*	Not present
Eulemur cinereiceps	Not present	*Lepilemur scottorum*	Not present
Eulemur collaris	*Eulemur fulvus collaris*	*Microcebus arnholdi*	Not present
Eulemur fulvus	*Eulemur fulvus fulvus*	*Phaner electromontis*	Not present
Eulemur macaco	*Eulemur macaco macaco*	*Phaner pallescens*	*Phaner furcifer pallescens*
Eulemur rufifrons	Not present	*Phaner parienti*	Not present
Eulemur rufus	*Eulemur fulvus rufus*	*Prolemur simus*	*Hapalemur simus*
Eulemur sanfordi	*Eulemur fulvus sanfordi*	*Propithecus candidus*	Not present
Hapalemur meridionalis	*Hapalemur griseus meridionalis*	*Propithecus perrieri*	Not present
Hapalemur occidentalis	*Hapalemur griseus occidentalis*	*Varecia variegata*	*Varecia variegata variegata*

Table A.8. Malagasy and Australian non-volant mammal species (not including primates) with a change in species name or which was absent from the Bininda-Emonds (2007) tree.

Species	Name in Bininda-Emonds tree	Species	Name in Bininda-Emonds tree
Madagascar			
Brachytarsomys villosa	Not present	*Microgale jobihely*	Not present
Eliurus antsingy	Not present	*Microgale majori*	Not present
Eliurus carletoni	Not present	*Microgale monticola*	Not present
Eliurus danieli	Not present	*Microgale nasoloi*	Not present
Eliurus grandidieri	Not present	*Microgale soricoides*	Not present
Hemicentetes nigriceps	Not present	*Microgale taiva*	Not present
Macrotarsomys petteri	Not present	*Monticolomys koopmani*	Not present
Microgale drouhardi	Not present	*Nesomys audeberti*	Not present
Microgale fotsifotsy	Not present	*Nesomys lambertoni*	Not present
Microgale grandidieri	Not present	*Voalavo antsahabensis*	Not present
Microgale gymnorhyncha	Not present	*Voalavo gymnocaudus*	Not present
Microgale jenkinsae	Not present		
Australia			
Antechinomys laniger	Not present	*Petrogale herberti*	Not present
Antechinus adustus	Not present	*Petrogale mareeba*	Not present
Antechinus agilis	Not present	*Petrogale purpureicollis*	Not present
Antechinus subtropicus	Not present	*Pseudochirulus cinereus*	Not present
Dasyuroides byrnei	Not present	*Pseudochirulus herbertensis*	*Pseudocheirus herbertensis*

Table A.9. Australian non-volant mammal species trait data included in the analyses. Trait details provided in Table A.5. Publication cut-off date for included sources of information was January 2013.*

Family	Species	Body mass (g) [a]	Arb. or Terr. [b]	Feeding guild [c]	Trophic level [d]	Loco. [e]	Activity period [f]	Habitat spec.	Torpor [g]
Order Dasyuromorphia									
Dasyuridae	*Antechinomys laniger*	28	Terr.	IN	2	TQ	Noct.	2	Yes
Dasyuridae	*Antechinus adustus*	28	Both	IN	2	Q	Noct.	1	dd
Dasyuridae	*Antechinus agilis*	22.1	Arb.	IN	2	AQ	Noct.	1	Yes
Dasyuridae	*Antechinus flavipes*	44.8	Terr.	IN	2	TQ	Noct.	3	Yes
Dasyuridae	*Antechinus godmani*	76.8	Terr.	IN	2	TQ	Noct.	1	dd
Dasyuridae	*Antechinus stuartii*	29.7	Arb.	IN	2	Q	Noct.	1	Yes
Dasyuridae	*Antechinus subtropicus*	33	Both	IN	2	Q	Noct.	2	dd
Dasyuridae	*Antechinus swainsonii*	65	Terr.	IN	2	TQ	Noct.	1	No
Dasyuridae	*Dasyuroides byrnei*	118.2	Terr.	CA	3	F	Noct.	1	Yes
Dasyuridae	*Dasyurus hallucatus*	484	Terr.	CA	3	Q	Noct.	4	No
Dasyuridae	*Dasyurus maculatus*	2599	Both	CA	3	Q	Noct.	1	No
Dasyuridae	*Ningaui yvonnae*	7.8	Terr.	IN	2	TQ	Noct.	1	Yes
Dasyuridae	*Phascogale tapoatafa*	195	Arb.	IN	2	AQ	Noct.	2	No
Dasyuridae	*Planigale gilesi*	9.44	Terr.	IN	2	TQ	Cath.	1	Yes
Dasyuridae	*Planigale ingrami*	6.44	Terr.	IN	2	TQ	Noct.	2	Yes
Dasyuridae	*Planigale maculata*	12.3	Terr.	IN	2	TQ	Noct.	4	Yes
Dasyuridae	*Planigale tenuirostris*	6.37	Terr.	IN	2	TQ	Noct.	3	Yes
Dasyuridae	*Sminthopsis archeri*	16	Terr.	IN	2	TQ	Noct.	1	dd
Dasyuridae	*Sminthopsis crassicaudata*	16.3	Terr.	IN	2	TQ	Noct.	2	Yes
Dasyuridae	*Sminthopsis douglasi*	55	Terr.	IN	2	TQ	Noct.	1	Yes
Dasyuridae	*Sminthopsis leucopus*	24	Terr.	IN	2	TQ	Noct.	1	No
Dasyuridae	*Sminthopsis macroura*	24	Terr.	IN	2	TQ	Noct.	3	Yes
Dasyuridae	*Sminthopsis murina*	17	Terr.	IN	2	TQ	Noct.	2	Yes
Dasyuridae	*Sminthopsis virginiae*	35	Terr.	IN	2	TQ	Noct.	1	dd

Family	Species	Body mass (g) [a]	Arb. or Terr. [b]	Feeding guild [c]	Trophic level [d]	Loco. [e]	Activity period [f]	Habitat spec.	Torpor [g]
Order Diprotodontia									
Acrobatidae	*Acrobates pygmaeus*	13.9	Both	OM	2	GAQ	Noct.	3	Yes
Burramyidae	*Cercartetus caudatus*	23	Arb.	OM	2	AQ	Noct.	1	Yes
Burramyidae	*Cercartetus concinnus*	14.1	Arb.	OM	2	AQ	Noct.	1	Yes
Burramyidae	*Cercartetus nanus*	27	Arb.	GU	1	AQ	Noct.	1	Yes
Hypsiprymnodontidae	*Hypsiprymnodon moschatus*	536	Terr.	OM	2	HL	Cath.	1	dd
Macropodidae	*Dendrolagus bennettianus*	10500	Both	FO	1	Q	Cath.	1	dd
Macropodidae	*Dendrolagus lumholtzi*	6650	Arb.	FO	1	AQ	Cath.	1	dd
Macropodidae	*Lagorchestes conspicillatus*	2820	Terr.	HE	1	HL	Noct.	1	No
Macropodidae	*Macropus agilis*	11900	Terr.	HE	1	HL	Noct.[1]	3	No
Macropodidae	*Macropus antilopinus*	27300	Terr.	HE	1	HL	Noct.	1	No
Macropodidae	*Macropus dorsalis*	11200	Terr.	HE	1	HL	Noct.	2	No
Macropodidae	*Macropus fuliginosus*	25600	Terr.	HE	1	HL	Cath.	1	No
Macropodidae	*Macropus giganteus*	33600	Terr.	HE	1	HL	Cath.	6	No
Macropodidae	*Macropus parma*	4160	Terr.	HE	1	HL	Noct.	1	No
Macropodidae	*Macropus parryi*	12700	Terr.	HE	1	HL	Noct.	4	No
Macropodidae	*Macropus robustus*	26000	Terr.	HE	1	HL	Noct.	5	No
Macropodidae	*Macropus rufogriseus*	16800	Terr.	HE	1	HL	Noct.	2	No
Macropodidae	*Macropus rufus*	39000	Terr.	HE	1	HL	Noct.	3	No
Macropodidae	*Onychogalea fraenata*	4940	Terr.	HE	1	HL	Noct.	1	No
Macropodidae	*Petrogale assimilis*	4650	Terr.	FO	1	HL	Noct.	1	No
Macropodidae	*Petrogale brachyotis*	4500	Terr.	HE	1	HL	Noct.	1	No
Macropodidae	*Petrogale herberti*	3977	Terr.	HE [2]	1	HL	Noct.	1	No
Macropodidae	*Petrogale inornata*	4570	Terr.	HE [2]	1	HL	Noct.	1	No
Macropodidae	*Petrogale mareeba*	3186	Terr.	HE [2]	1	HL	Noct.	1	No
Macropodidae	*Petrogale penicillata*	6960	Terr.	HE	1	HL	Noct.	2	No
Macropodidae	*Petrogale purpureicollis*	5700	Terr.	HE [3]	1	HL	Noct.	1	No
Macropodidae	*Petrogale xanthopus*	8500	Terr.	HE	1	HL	Noct.	1	No
Macropodidae	*Thylogale stigmatica*	4540	Terr.	FO	1	HL	Cath.	3	No

Family	Species	Body mass (g) [a]	Arb. or Terr. [b]	Feeding guild [c]	Trophic level [d]	Loco. [e]	Activity period [f]	Habitat spec.	Torpor [g]
Macropodidae	*Thylogale thetis*	5400	Terr.	FO	1	HL	Noct.	1	No
Macropodidae	*Wallabia bicolor*	15000	Terr.	HE	1	HL	Noct.	3	No
Petauridae	*Dactylopsila trivirgata*	413	Arb.	IN	2	AQ	Noct.	1	No
Petauridae	*Petaurus australis*	571	Arb.	GU	1	GAQ	Noct.	3	No
Petauridae	*Petaurus breviceps*	119	Arb.	OM	2	GAQ	Noct.	4	Yes
Petauridae	*Petaurus gracilis*	362	Arb.	OM	2	GAQ	Noct.	1	dd
Petauridae	*Petaurus norfolcensis*	230	Arb.	OM	2	GAQ	Noct.	3	No
Phalangeridae	*Trichosurus caninus*	3140	Arb.	FO	1	AQ	Noct.	1	No
Phalangeridae	*Trichosurus vulpecula*	2700	Arb.	FO	1	AQ	Noct.	5	No
Phascolarctidae	*Phascolarctos cinereus*	6580	Arb.	FO	1	AQ	Noct.	4	No
Potoridae	*Aepyprymnus rufescens*	2800	Terr.	OM	2	HL	Noct.	3	No
Potoridae	*Bettongia lesueur*	1450	Terr.	OM	2	F	Noct.	1	No
Potoridae	*Potorous longipes*	1840	Terr.	OM	2	HL	Noct.	1	No
Potoridae	*Potorous tridactylus*	1090	Terr.	OM	2	HL	Noct.	1	No
Pseudocheiridae	*Hemibelideus lemuroides*	1000	Arb.	FO	1	AQ	Noct.	1	No
Pseudocheiridae	*Petauroides volans*	1260	Arb.	FO	1	GAQ	Noct.	4	No
Pseudocheiridae	*Petropseudes dahli*	1880	Both	FO	1	TQ	Noct.	1	dd
Pseudocheiridae	*Pseudocheirus peregrinus*	894	Arb.	FO	1	AQ	Noct.	3	No
Pseudocheiridae	*Pseudochirops archeri*	1150	Arb.	FO	1	AQ	Noct.	1	dd
Pseudocheiridae	*Pseudochirulus cinereus*	1000	Arb.	FO	1	AQ	Noct.	1	Yes
Pseudocheiridae	*Pseudochirulus herbertensis*	900	Arb.	FO	1	AQ	Noct.	1	dd
Vombatidae	*Vomabatus ursinus*	27192	Terr.	HE	1	TQ	Noct.	1	No
Order Monotremata									
Ornithorhynchidae	*Ornithorhynchus anatinus*	1480	Terr.	IN	2	SA	Cath.	2	No
Tachyglossidae	*Tachyglossus aculeatus*	2140	Terr.	IN	2	F	Cath.	5	Yes
Order Peramelemorphia									
Peramelidae	*Isoodon auratus*	485	Terr.	OM	2	TQ	Noct.	1	No
Peramelidae	*Isoodon macrourus*	1510	Terr.	OM	2	TQ	Noct.	4	No
Peramelidae	*Isoodon obesulus*	825	Terr.	OM	2	TQ	Noct.[3]	1	No

Family	Species	Body mass (g) [a]	Arb. or Terr. [b]	Feeding guild [c]	Trophic level [d]	Loco. [e]	Activity period [f]	Habitat spec.	Torpor [g]
Peramelidae	*Perameles nasuta*	720	Terr.	IN	2	TQ	Noct.	2	No
Thylacomyidae	*Macrotis lagotis*	1859	Terr.	OM	2	F	Noct.	1	No
Order Rodentia									
Muridae	*Conilurus penicillatus*	175.2	Arb.	GR	1	AQ	Noct.	1	dd
Muridae	*Hydromys chrysogaster*	626	Terr.	CA	3	SA	Noct.	4	No
Muridae	*Leggadina forresti*	23.9	Terr.	GR	1	F	Noct.	2	Yes
Muridae	*Leggadina lakedownensis*	17.5	Terr.	OM	2	TQ	Noct.	1	dd
Muridae	*Leporillus conditor*	329	Terr.	FO	1	TQ	Noct.	1	dd
Muridae	*Melomys burtoni*	71.3	Arb.	OM	2	AQ	Noct.	3	dd
Muridae	*Melomys capensis*	70	Both	dd	dd	dd	Noct.	1	dd
Muridae	*Melomys cervinipes*	71.2	Arb.	FO	1	AQ	Noct.	3	dd
Muridae	*Notomys cervinus*	34.8	Terr.	OM	2	HL	Noct.	1	No
Muridae	*Pseudomys bolami*	15.5	Terr.	OM	2	F	Noct.	1	dd
Muridae	*Pseudomys delicatulus*	8.56	Terr.	GR	1	TQ	Noct.	3	dd
Muridae	*Pseudomys desertor*	37.1	Terr.	OM	2	F	Noct.	2	dd
Muridae	*Pseudomys fumeus*	68.7	Terr.	OM	2	F	Noct.	1	dd
Muridae	*Pseudomys gracilicaudatus*	79.6	Terr.	OM	2	TQ	Noct.	4	No
Muridae	*Pseudomys hermannsburgensis*	14.3	Terr.	OM	2	TQ	Noct.	3	No
Muridae	*Pseudomys nanus*	70.4	Terr.	GR	1	TQ	Noct.	1	dd
Muridae	*Pseudomys novaehollandiae*	16.8	Terr.	GR	1	TQ	Noct.	1	dd
Muridae	*Pseudomys oralis*	95	Terr.	OM	2	TQ	Noct.	1	dd
Muridae	*Pseudomys patrius*	15	Terr.	dd	dd	TQ	Noct.	2	dd
Muridae	*Pseudomys shortridgei*	70	Terr.	FO	1	TQ	Noct.	1	dd
Muridae	*Rattus fuscipes*	125	Terr.	OM	2	TQ	Noct.	3	No
Muridae	*Rattus leucopus*	201	Terr.	OM	2	TQ	Noct.	2	No
Muridae	*Rattus lutreolus*	106	Terr.	OM	2	TQ	Cath.	2	No
Muridae	*Rattus sordidus*	157	Terr.	HE	1	TQ	Noct.	3	No
Muridae	*Rattus tunneyi*	169	Terr.	HE	1	TQ	Noct.	3	No
Muridae	*Rattus villosissimus*	222	Terr.	OM	2	TQ	Noct.	3	No

Family	Species	Body mass (g) [a]	Arb. or Terr. [b]	Feeding guild [c]	Trophic level [d]	Loco. [e]	Activity period [f]	Habitat spec.	Torpor [g]
Muridae	*Uromys caudimaculatus*	644	Terr.	OM	2	TQ	Diurn.	2	No
Muridae	*Xeromys myoides*	45.2	Terr.	CA	3	TQ	Noct.	1	dd
Muridae	*Zyzomys argurus*	40.4	Terr.	OM	2	TQ	Noct.	3	dd

Abbreviations: Terr., terrestrial; Arb., arboreal; Both, terrestrial and arboreal; CA, carnivore; FO, folivore; GR, granivore; GU, gumnivore; HE; herbivore; IN, insectivore; OM, omnivore; Loco., locomotion; AQ, arboreal quadruped; F, fossorial; GAQ, gliding arboreal quadruped; Q, arboreal and terrestrial quadruped; SA, semi-aquatic; TQ, terrestrial quadruped; Diurn., diurnal; Noct., nocturnal; Cath., cathemeral; spec., specificity; dd, data deficient.

[*] Traits from the most recent studies prior to the cut-off date are provided. Published data compilations were used where possible and supplementary references are provided for species not present in large published datasets. Literature searches were completed in Google Scholar and Web of Science.

[a] Hanna and Cardillo 2014; Jones et al. 2009, Nowak 2005

[b] Department of the Environment 2015; Jones et al. 2009; Maxwell et al. 1996; McNab 2008; Nowak 1999, 2005; *Rodentia*: Cronin 2008; Dyck and Strahan 2006; Flannery 1990b, 1995; Fimbel et al. 2011; Firth et al. 2005; NPWS 2002; Wood 1971

[c] Department of the Environment 2015; Jones et al. 2009; Maxwell et al. 1996; McNab 2008; Nowak 1999, 2005; *Dasyuromorphia:* Fox and Archer 1984; Menna 2003; Scarff et al. 1998; *Diprotodontia*: Baxter et al. 2001; Carter and Goldizen 2003; Carthew et al. 1999; Ellis et al. 1992; Horsup and Marsh 1992; Pestell and Petit 2007; Rawlins and Handasyde 2002; Read and Fox 1991; Ritchie et al. 2008; Sprent and McArthur 2002; Stefano and Newell 2008; Stirrat 2002; Telfer and Bowman 2006 Wahungu et al. 1999; *Monotremata*: McLachlan-Troup et al. 2010; *Rodentia:* Cronin 2008; Dyck and Strahan 2006; Flannery 1990b, 1995; Fimbel et al. 2011; Firth et al. 2005; NPWS 2002; Pineda-Munoz and Alroy 2014; Wood 1971

[d] 1 = primary consumer; 2 =secondary consumer; 3= tertiary consumer

[e] Nowak 1999, 2005; *Dasyuromorphia:* Menna 2003; *Rodentia*: Dawson and Fanning 1981; NPWS 2002

[f] Bennie et al. 2014; Department of the Environment 2015; Jones et al. 2009; Kirk 2006; Nowak 2005; *Monotremata*: Bethge et al. 2009; *Rodentia:* Cronin 2008; Dawson and Fanning 1981; Van Dyck and Strahan 2006; Fanning and Dawson 1980; Flannery 1990b, 1995; Fimbel et al. 2011; Firth et al. 2005; Pineda-Munoz and Alroy 2014; Roll et al. 2006; Watts and Aslin 1981; Wood 1971

[g] Geiser 1994; Geiser and Baudinette 1987; Hanna and Cardillo 2014; McNab 2008; Reik and Geiser 2014; Rojas et al. 2014; Turbill et al. 2011; *Monotremata*: Grigg et al. 1992

[1] has some diurnal activity, but not described as cathemeral in the literature, predominantly nocturla activity pattern (Stirrat 2004)

[2] part of a complex of multiple *Petrogale* species in East Queensland (Eldridge et al. 2008); diet data taken from Turner (2004) due to individual descriptions

[3] used to be a subspecies of *Petrogale lateralis* (Eldridge et al. 2001), diet data taken from Eldridge (2012)
[4] suggested to be diurnal in captivity and at sites with no predators, however, data are inconclusive (Warnecke et al. 2007)

References

Ackerly, D.D., and Cornwell, W.K. (2007). A trait-based approach to community assembly, partitioning of species trait values into within- and among-community components. Ecology Letters. 10, 135-145.

Ackerly, D.D. (2003). Community assembly, niche conservatism, and adaptive evolution in changing environments. International Journal of Plant Sciences. 164(S3), 165-184.

Adler, P. (2004). Neutral models fail to reproduce observed species-area and species-time relationships in Kansas grasslands. Ecology. 85(5), 1265-1272.

Adler, P.B., HilleRisLambers, J., and Levine, J.M. (2007). A niche for neutrality. Ecology Letters.10, 95-104.

Albert, C.H., Thuiller, W., Yoccoz, N.G., Douzet, R., Aubert, S., and Lavorel, S. (2010). A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits. Functional Ecology. 24(6), 1192-1201.

Albignac, R. (1972). The Carnivora of Madagascar. In Battistini, R. and Richard-Vindard, G. (Eds.). *Biogeography and Ecology of Madagascar* (Pp. 667-682). The Hague: Dr W. Junk.

Albignac, R. (1974). Observations éco-éthologiques sur le genre Eupleres, Viverridé de Madagascar. Extrait de la Terre et la Vie, Revue d'Ecologie Appliquée. 28, 321-351.

Albignac, R. (1984). The carnivores. In Jolly, A., Oberle, P. and Albignac, R. (Eds.). *Key Environments- Madagascar* (Pp. 167-181). Oxford: Pergamon Press.

Albrecht, G.H., Jenkins, P.D., and Godfrey, L.R. (1990). Ecogeographic size variation among the living and subfossil prosimians of Madagascar. American Journal of Primatology. 22, 1-50.

Ali, J.R., and Huber, M. (2010). Mammalian biodiversity on Madagascar controlled by ocean currents. Nature. 463, 653-56.

Alonso, D., Etienne, R.S., and McKane, A.J. (2006). The merits of neutral theory. Trends in Ecology and Evolution. 21(8), 451-457.

Alonso, L.E., Schulenberg, T.S., Radolife, S., and Missa, O. (2002). Une evaluation biologique de la Réserve Naturelle Intégrale d'Ankarafantsika, Madagascar. Bulletin RAP d'Evaluation Rapide. 23, 1-139.

Amori, G. and Luiselli, L. (2011). Small mammal community structure in West Africa, a meta-analysis using null models. African Journal of Ecology. 49(4), 418-430.

Anderson, T. M., Shaw, J., and Olff, H. (2011). Ecology's cruel dilemma, phylogenetic trait evolution and the assembly of Serengeti plant communities. Journal of Ecology. 99(3), 797-806.

Andriaholinirina, N., Baden, A., Blanco, M., Chikhi, L., Cooke, A., Davies, N., Dolch, R., Donati, G., Ganzhorn, J., Golden, C., Groeneveld, L.F., Irwin, M., Johnson, S., Kappeler, P., King, T., Lewis, R., Louis, E.E., Markolf, M., Mass, V., Mittermeier, R.A., Nichols, R., Patel, E., Rabarivola, C.J., Raharivololona, B., Rajaobelina, S., Rakotoarisoa, G., Rakotomanga, B., Rakotonanahary, J., Rakotondrainibe, H., Rakotondratsimba, G., Rakotondratsimba, M., Rakotonirina, L., Ralainasolo, F.B., Ralison, J., Ramahaleo, T., Ranaivoarisoa, J.F., Randrianahaleo, S.I., Randrianambinina, B., Randrianarimanana, L., Randrianasolo, H., Randriatahina, G., Rasamimananana, H., Rasolofoharivelo, T., Rasoloharijaona, S., Ratelolahy, F., Ratsimbazafy, J., Ratsimbazafy, N., Razafindraibe, H., Razafindramanana, J., Rowe, N., Salmona, J., Seiler, M., Volampeno, S., Wright, P., Youssouf, J., Zaonarivelo, J. and Zaramody, A. 2014. *Propithecus diadema*. The IUCN Red List of Threatened Species. Version 2014.3. <www.iucnredlist.org>. Downloaded on 15 February 2015.

Andriaholinirina, N., Fausser, J.L., Roos, C., Zinner, D., Thalmann, U., Rabarivola, C., Ravoarimanana, I., Ganzhorn, J.U., Meier, B., Hilgartner, R., Walter, L., Zaramody, A., Langer, C., Hahn, T., Zimmermann, E., Radespiel, U., Craul, M., Tomiuk, J., Tattersall, I., and Rumpler, Y. (2006). Molecular phylogeny and taxonomic revision of the sportive lemurs (*Lepilemur*, Primates). BMC Evolutionary Biology. 6, 17.

Andrianjakarivelo, V., Razafimahatratra, E., Razafindrakoto, Y., and Goodman, S.M. (2005). The terrestrial small mammals of the Parc National de Masoala, northeastern Madagascar. Acta Theriologica. 50, 537-549.

Andriantompohavana, R., Lei, R., Zaonarivelo, J.R., Engberg, S.E., Nalanirina, G., McGuire, S.M., Shore, G.D., Andrianasolo, J., Herrington, K., Brenneman, R.A., and Louis, E.E. (2007). Molecular phylogeny and taxonomic revision of the woolly lemurs, genus *Avahi* (Primates, Lemuriformes). Occasional papers, museum of Texas Tech University 51, 1-59.

Angermeier, P.L., and Winston, M.R. (1998). Local vs. regional influences on local diversity in stream fish communities of Virginia. Ecology. 79, 911-927.

Archer, M. Arena, R, Bassarova, M., Black, K. Brammall, J., Cooke, B., Creaser, P., Crosby, K., Gillespie, A., Godthelp, H., Gott, M., Hand, S.J., Kear, B., Krikmann, A., Mackness, B., Muirhead, J., Musser, A., Myers, T., Pledge, N., Wang, Y., and Wroe, S. (1999). The evolutionary history and diversity of Australian mammals. Australian Mammalogy. 2l, 1-45.

Arita, H.T, and Rodriguez, P. (2002). Geographic range, turnover rate and the scaling of species diversity. Ecography. 25(5), 541-550.

Arnold, C., Matthews, L.J., and Nunn, C.L. (2010). The 10kTrees website, a new online resource for primate phylogeny. Evolutionary Anthropology. 19, 114-118.

Avise, J.C. (2000). *Phylogeography, the History and Formation of Species*. Cambridge, MA: Harvard University Press.

Ayres, J.M., and Clutton-Brock, T.H. 1992. River boundaries and species range size in Amazonian primates. American Naturalist.140, 531-537.

Badgley, C., and Fox, D.L. (2000). Ecological biogeography of North American mammals, species density and ecological structure in relation to environmental gradients. Journal of Biogeography. 27(6), 1437-1467.

Baillie, J. (1996). Analysis. In J. Baillie and B. Groombridge (Eds.). *1996 IUCN Red List of Threatened Animals* (Pp. 24-43). Gland, Switzerland: IUCN.

Balko, E.A. (1996). Foraging ecology of *Varecia variegata* at Ranomafana National Park, Madagascar. American Journal of Primatology. 22, 64.

Bannar-Martin, K.H. (2013). Using spatial structural equation modeling as a novel approach to understanding primate community composition and diversity. American Journal of Physical Anthropology. 150(S56), 73-74.

Bannar-Martin, K.H. (2014). Primate and nonprimate mammal community assembly, the influence of biogeographic barriers and spatial scale. International Journal of Primatology. 35, 1122-1142.

Barden, T. L., Evans, M. I., Raxworthy, C. J., Razafimahaimodison, J.-C., and Wilson, A. (1991). The mammals of Ambatovaky Special Reserve. In Thompson, P. M., and M. I. Evans (Eds.). *A survey of Ambatovaky Special Reserve, Madagascar* (pp. 5.1-5.20). London: Madagascar Environmental Research Group.

Barnosky, A.D., Carrasco, M.A., and Davis, E.B. (2005). The Impact of the Species–Area Relationship on Estimates of Paleodiversity. PLOS Biology. 3(8), e266. doi:10.1371/journal.pbio.0030266

Barot, S., Heino, M., and O'Brien, L. (2004). Estimating reaction norms for age and size at maturation when age at first reproduction is unknown. Evolutionary Ecology. 6, 659-678.

Baselga, A. (2008). Determinants of species richness, endemism and turnover in European longhorn beetles. Ecography. 31, 263-271

Baudinette, R.V. (1994). Locomotion in Macropodoid Marsupials - Gaits, Energetics and Heat-Balance. Australian Journal of Zoology. 42, 103-123.

Baxter, G., Moll, E., and Lisle, A. (2001). Pasture grazing by black-striped wallabies (*Macropus dorsalis*) in central Queensland. Wildlife Research. 28, 269-276.

Beaudrot, L.H., and Marshall, A.J. (2011). Primate communities are structured more by dispersal limitation than by niches. Journal of Animal Ecology. 80(2), 332-341.

Beaudrot, L.H, Rejmanek, M., and Marshall, A.J. (2013a). Dispersal modes affects tropical forest assembly across trophic levels. Ecography. 36(9), 984-993.

Beaudrot, L.H., Struebig, M. J., Meijaard, E., van Balen, B., Husson, S., and Marshall, A.J. (2013b). Co-occurrence patterns of Bornean vertebrates suggest competitive exclusion is strongest among distantly related species. Oecologia. 173, 1053-1062.

Beaudrot, L.H., Struebig, M. J., Meijaard, E., Van Balen, S., Husson, S., Young, C.F., and Marshall, A.J. (2013c). Interspecific interactions between primates, birds, bats, and squirrels may affect community composition on Borneo. American Journal of Primatology. 75(2), 170-185.

Beaudrot, L., Kamilar, J.M., Marshall, A.J., and Reed, K.E (2014). African primate assemblages exhibit a latitudinal gradient in dispersal limitation. International Journal of Primatology. 35, 1088-1104.

Bell, G. 2001. Neutral macroecology. Science. 293, 2413-2418.

Belmaker, J., and Jetz, W. (2013). Spatial scaling of functional structure in bird and mammal assemblages. The American Naturalist. 18, 466-478.

Bennie, J.J., Duffy, J.P., Inger, R., and Gaston, K.J. (2014). Biogeography of time partitioning in mammals. Proceedings of The National Academy Of Sciences, 111(38), 13727-13732.

Benstead, J.P, Barnes, K.H., and Pringle, C.M. (2001). Diet, activity patterns, foraging movements and response to deforestation of the Aquatic Tenrec, *Limnogale mergulus* (Lipotyphla, Tenrecidae) in eastern Madagascar. Journal of Zoology. 254, 119-129.

Bernard-Verdier, M., Flores, O., Navas, M.-L., and Garnier, E. (2013). Partitioning phylogenetic and functional diversity into alpha and beta components along an environmental gradient in a Mediterranean rangeland. Journal of Vegetation Science. 24, 877-889.

Bethge, P., Munks, S., Otley, H., and Nicol, S. (2009). Activity patterns and sharing of time and space of platypuses, *Ornithoryhynchus anatinus*, in a subalpine Tasmanian Lake. Journal of Mammology. 90(6), 1350-1356.

Biebouw, K. (2009). Home range size and use in *Allocebus trichotis* in Analaamazaotra Special Reserve, Central Eastern Madagascar. International Journal of Primatology. 30, 367-386.

Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E. MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., Price, S. A., Vos, R. A., Gittleman, J. L., and Purvis, A. (2007). The delayed rise of present-day mammals. Nature. 446, 507-512.

Birkinshaw, C., and Colquhoun, I.C. (2003). Lemur food plants. In S.M. Goodman and J.P. Benstead (Eds.). *The Natural History of Madagascar* (Pp. 1207-1221). Chicago: The University of Chicago Press.

Blanc-Pamard, C. (2009). The Mikea Forest under threat (southwest Madagascar): how public policy leads to conflicting territories. Field Actions Science Report. 2-12.

Blanchet, F.G., Legendre, P., and Borcard, D. (2008). Forward selection of explanatory variables. Ecology. 89(9), 2623-2632.

Blanco, M.B., and Rahalinarivo, V. (2010). First direct evidence of hibernation in an eastern dwarf lemur species (*Cheirogaleus crossleyi*) from the high-altitude forest of Tsinjoarivo, central-eastern Madagascar. Naturwissenschaften. 97, 945-950.

Blanco, M.B., Godfrey, L.R., Rakotondratsima, M., Rahalinarivo, V., Samonds, K.E., Raharison, J.-L., and Irwin, M.T. (2009). Discovery of sympatric dwarf lemur species in the high-altitude rain forest of Tsinjoarivo, eastern Madagascar, implications for biogeography and conservation. Folia Primatologica. 80, 1-17.

Borcard, D., Legendre, P., and Drapeau, P. (1992). Partialling out the spatial component of ecological variation. Ecology. 73, 1045-1055.

Borcard, D., and Legendre, P. (1994). Environmental control and spatial structure in ecological communities, an example using oribatid mites (*Acari, Oribatei*). Environmental and Ecological Statistics. 1(1), 37-61.

Borcard, D., and Legendre, P. (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling. 153(1-2), 51-68.

Borcard, D., Gillet, F., and Legendre, P. (2011). *Numerical Ecology with R*. New York: Springer.

Borcard, D., Legendre, P., Avois-Jacquet, C., and Tuomisto, H. (2004). Dissecting the spatial structure of ecological data at multiple scales. Ecology. 85(7), 1826-1832.

Booth, B.D., and Larson, D.W. (1999). Impact of language, history, and choice of system on the study of assembly rules. In E. Weiher and P. Keddy (Eds.). *Ecological Assembly Rules, Perspectives, Advances, Retreats* (Pp. 206-229). Cambridge, UK: Cambridge University Press.

Botta-Dukat, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. Journal of Vegetation Science. 16, 533-540.

Boumans, L., Vieites, D.R., Glaw, F., and Vences, M. (2007). Geographic patterns of deep mitochondrial differentiation in widespread Malagasy reptiles. Molecular Phylogenetics and Evolution. 45(3), 822-839.

Bourlière, F. (1985). Primate communities, their structure and role in tropical ecosystmes. International Journal of Primatology. 6, 1-26.

Bousquet, B., and Rabetaliana, H. (1992). Site du patrimoine mondial des Tsingy de Bemaraha et autres sites d'intérêt biologique et ecologique du Fivondronanana d'Antsalova. Paris: UNESCO.

Bowler, J.M., Johnston, H., Olley, J.M., Prescott, J.R., Roberts, R.G., Shawcross, W., and Spooner, N.A. (2003). New ages for human occupation and climatic change at Lake Mungo, Australia. Nature. 421, 837-840.

Britt, A., and Virkaitis, V. (2003). Brown-tailed Mongoose *Salanoia concolor* in the Betampona Reserve, eastern Madagascar, photographs and an ecological comparison with Ring-tailed Mongoose *Galidia elegans*. Small Carnivore Conservation. 28, 1-3.

Brown, J.H. (1971). Mammals on mountaintops, nonequilibrium insular biogeography. The American Naturalist. 105(945), 467-478.

Brown, J.H. (1978). The theory of island biogeography and the distribution of boreal birds and mammals. Great Basin Naturalist Memoirs. 2, 209-227.

Buckley, L.B., Davies, T.J., Ackerly, D.D., Kraft, N.J.B., Harrison, S.P., Anacker, B.L., Cornell, H.V., Damschen, E.I., Grytness, J.-A., Hawkins, B.A., McCain, C.M., Stephens, P.R., and Wiens, J.J. (2010). Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. Proceedings of the Royal Society B, Biological Sciences. 277(1691), 2131-2138.

Burgess, N.D., D'Amico Hales, J., Underwood, E.C., Dinerstein, E., Olson, D., Itoua, I., Schipper, J., Ricketts, T.H., and Newman, K. (2004). *Terrestrial Ecoregions of Africa and Madagascar: A Conservation Assessment*, Washington, DC: Island Press.

Burney, D.A. (1996). Climate change and fire ecology as factors in the quaternary biogeography of Madagascar. In W.R. Lourenco (Ed.). *Biogeographie de Madagascar* (Pp. 49-58). Paris: Editions de l'ORSTROM.

Burney, D.A. (1997). Theories and facts regarding Holocene environmental change before and after human colonization. In S.M. Goodman and B.D. Patterson (Eds.), *Natural Change and Human Impact in Madagascar* (Pp. 75-89). Washington: Smithsonian Press.

Burney, D.A. (2004). A chronology for late prehistoric Madagascar. Journal of Human Evolution. 47(1-2), 25-63.

Burney, D.A., and MacPhee, R.D.E. (1988). Mysterious island: what killed Madagascar's large native animals? Natural History. 97(7), 46-55.

Burney D. A., Robinson, G. S., and Pigott, L. (2003). *Sporormiella* and the late Holocene extinctions in Madagascar. Proceedings of the National Academy of Sciences, 100(19), 10800-10805.

Cadotte, M.W. (2007). Concurrent niche and neutral processes in the competition-colonization model of species coexistence. Proceedings of the Royal Society B, Biological Sciences. 274(1626), 2739-2744.

Cadotte, M.W., Carscadden, K., and Mirotchnick, N. (2011). Beyond species, functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology. 48(5), 1079-1087.

Cailliez, F. (1983). The analytical solution of the additive constant problem. Psychometrika. 48, 305-308.

Calba, S., Maris, V., and Devictor, V (2014). Measuring and explaining large-scale distribution of functional and phylogenetic diversity in birds, separating ecological drivers from methodological choices. Global Ecology and Biogeography. 23(6), 669-678.

Caley, M. J., and D. Schluter. (1997). The relationship between local and regional diversity. Ecology. 78, 70-80.

Cannon, C.H., and Leighton, M. (1994). Comparative locomotor ecology of gibbons and macaques, selection of canopy elements for crossing gaps. American Journal of Physical Anthropology. 93, 505-524.

CAPAD (2008). Collaborative Australian Protected Areas Database (CAPAD) 2008, Commonwealth of Australia 2008, Retrieved 7 February 2014.

Cardillo, M. (2011). Phylogenetic structure of mammal assemblages at large geographical scales, linking phylogenetic community ecology with macroecology. Philosophical Transactions of the Royal Society B, Biological Sciences, 366(1577), 2545-2553.

Cardillo, M., and Brohman, L. (2001). Body size and risk of extinction in Australian mammals. Conservation Biology. 15(5), 1435-1440.

Cardillo, M., Gittleman, J. L., and Purvis, A (2008). Global patterns in the phylogenetic structure of island mammal assemblages. Proceedings of the Royal Society B, Biological Sciences. 275(1642), 1549-1556.

Cardillo, M., and Meijaard, E. (2010). Phylogeny and co-occurrence of mammal species on Southeast Asian islands. Global Ecology and Biogeography. 19, 465-474.

Carleton, M.D. (1994). Systematic studies of Madagascar's endemic rodents (Muroidea, Nesomyinae), revision of the genus *Eliurus*. American Museum Novitates. 3087, 1-55.

Carleton, M.D. (2003). *Eliurus*, tufted-tailed rats. In S.M. Goodman, and J.P. Benstead (Eds.). *The Natural History of Madagascar (*Pp. 1373-1380). Chicago: The University of Chicago Press.

Carleton, M.D., and Goodman, S.M. (1996). Systematic studies of Madagascar's endemic rodents (Muroidea, Muridae), a new genus and species from the Central Highlands. Fieldiana Zoology. 85, 231-256.

Carleton, M.D., and Goodman, S.M. (1998). New taxa of nesomyine rodents (Muroidea, Muridae) from Madagascar's northern highlands, with taxonomic comments on previously described forms. A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar, with reference to elevational variation (ed. by S.M. Goodman). Fieldiana Zoology. 90, 163-200.

Carleton, M.D., and Goodman, S.M. (2000). Rodents of the Parc national de Marojejy, Madagascar. Fieldiana Zoology. 97, 231-263.

Carleton, M.D., and Goodman, S.M. (2003). *Macrotarsomys*, Big-footed Mice. In, S.M. Goodman and J.P. Benstead (Eds.). *The Natural History of Madagascar* (Pp. 1386-1388). Chicago: The University of Chicago Press.

Carleton, M.D., and Goodman, S.M. (2007). A New Species of the *Eliurus majori* Complex (Rodentia, Muroidea, Nesomyidae) from South-central Madagascar, with Remarks on Emergent Species Groupings in the Genus *Eliurus*. American Museum Novitates. 3547, 1-21.

Carleton, M.D., Goodman, S.M., and Rakotondravony, D. (2001). A new species of tufted-tailed rat, genus *Eliurus* (Muridae, Nesomyinae), from western Madagascar, with notes on the distribution of *E. myoxinus*. Proceedings of the Biological Society of Washington. 114, 972-987.

Carlson, M.L., Flagstad, L.A., Gillet, F., and Mitchell, E.A.D. (2010). Community development along a proglacial chronosequence: are above-ground and below-ground community structure controlled more by biotic than abiotic factors Journal of Ecology. 98(5), 1084-1095.

Carter, K., and Goldizen, A. (2003). Habitat choice and vigilance behavior of brush-tailed rock-wallabies (*Petrogale penicillata*) within their noctural foraging ranges. Wildlife Research. 30, 355-364.

Carthew, S.M., Goldingay, R.L., and Funnell, D.L. (1999). Feeding behaviour of the yellow-bellied glider (*Petaurus australis*) at the western edge of its range. Wildlife Research. 26, 199-208.

Cavender-Bares, J., Ackerly, D. D., Baum, D. A., and Bazzaz, F. A. (2004). Phylogenetic overdispersion in Floridian oak communities. The American Naturalist. 163(6), 823-843.

Cavender-Bares, J., Keen, A., and Miles, B. (2006). Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. Ecology. 87, S109-S122.

Cavender-Bares, J., Kozak, K., and Fine, P. (2009). The merging of community ecology and phylogenetic biology. Ecology. 12, 693-715.

Cawood, P. A., and Korsch, R. J. (2008). Assembling Australia, Proterozoic building of a continent. Precambrian Research. 166(1-4), 1-35.

Ceballos, G., and Brown, J.H. (1995). Global patterns of mammalian diversity, endemism, and endangerment. Conservation Biology. 9(3), 559-568.

Chalcraft, D.R., Williams, J., Smith, M.D., and Willig, M.R. (2004). Scale dependence in the species richness-productivity relationship, the role of species turnover. Ecology. 85, 2701-2708.

Chan, L.M., Brown, J.L., and Yoder, A.D. (2011). Integrating statistical genetic and geospatial methods brings new power to phylogeography. Molecular Phylogenetics and Evolution. 59(2), 523-537.

Chapman, C.A., Struhsaker, T.T., Skorupa, J. P., Snaith, T.V., and Rothman, J.M. (2010). Understanding long-term primate community dynamics: implications of forest change. Ecological Applications. 20, 179-191.

Chase, J.M. (2003). Community assembly, when should history matter. Oecologia. 136(4), 489-498.

Chase, J.M. (2007). Drought mediates the importance of stochastic community assembly. Proceedings of the National Academy of Sciences. 104(44), 17430-17434.

Chase, J.M. (2010). Stochastic Community assembly causes higher biodiversity in more productive environments. Science. 328(5984), 1388-1391.

Chase, J.M., Amarasekare, P., Cottenie, K., Gonzalez, A., Holt, R.D., Holyoak, M., Hoopes, M.F., Leibold, M.A., Loreau, M., Mouquet, N., Shurin, J.B., and Tilman, D. (2005). Competing Theories for Competitive Metacommunities. In M. Leibold, R. Holt and M. Holyoak (Eds.). *Metacommunity Ecology* (Pp. 335-354). Chicago: University of Chicago Press.

Chase, J.M., and Leibold, M.A. (2003). *Ecological Niches, Linking Classical and Contemporary Approaches.* Chicago: University of Chicago Press.

Chase, J.M., and Myers, J.A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. Philosophical Transactions of the Royal Society B, Biological Sciences. 366(1576), 2351-2363.

Chase, J.M., Biro, E.G., Ryberg, W.A., and Smith, K.G. (2009). Predators temper the relative importance of stochastic processes in the assembly of prey metacommunities. Ecology Letters. 12, 1210-1218.

Chave, J. (2004). Neutral theory and community ecology. Ecology Letters. 7(3), 241-253.

Chave, J., and Leigh, Jr, E.G., (2002). A spatially-explicit model of betadiversity in tropical forests. Theoretical Population Biology. 62, 153-168.

Chu, C.J., Wang, Y.-S., Du, G.-Z., Maestre, F.T., Luo, Y.-J., and Wang, G. (2007). On the balance between niche and neutral processes as drivers of community structure along a successional gradient, insights from alpine and sub-alpine meadow communities. Annnals of Botany. 100, 807-812.

Cianciaruso, M.V. (2011). Beyond taxonomical space, large-scale ecology meets functional and phylogenetic diversity. Frontiers of Biogeography. 3, 87-90.

Clark, D.A., Piper, S.C., Keeling, C.D., and Clark, D.B. (2003).Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984-2000. Proceedings of the National Academy of Sciences USA. 100, 5852-5857.

Clements, F.E. (1916). *Plant Succession, an Analysis of the Development Of Vegetation.* Washington, DC: Carnegie Institution of Washington.

Clutton-Brock, T.H., and Harvey, P.H. (1977). Species differences in feeding and ranging behaviour in primates. American Society of Mammalogists. S7, 532-563.

Clutton-Brock, T.H., and Harvey, P.H. (1983). The functional significance of variation in body size among mammals. In T. H. Clutton-Brock (Ed.). *Primate Ecology* (Pp. 557-584). New York: Academic Press.

Colquhoun, I.C. (2007). Strategies of Cathemeral Primates. In Gursky-Doyen, S.and Nekaris, K.A.I. *Primate Anti-Predator Strategies* (Pp. 148-149). New York: Springer.

Colwell, R.K., and Lees, D.C. (2000). The mid-domain effect, geometric constraints on the geography of species richness. Trends in Ecology and Evolution. 15, 70-76.

Condit, R., Pitman, N., Leigh, E.G., Chave, J., Terborgh, J., Foster, R.B., Núñez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E., and Hubbell, S.P. (2002). Beta-diversity in tropical forest trees. Science. 295(5555), 666-669.

Connell, J.H., and R.O. Slatyer. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist. 111, 1119-1144.

Connor, E.F., and Simberloff, D. (1979). You can't falsify ecological hypotheses without data. Bulletin of the Ecologocal Society of America. 60, 154-155.

Conservation Breeding Specialist Group (SSC/IUCN). (2002). Evaluation et plans de gestion pour la conservation (CAMP) de la faune de Madagascar, lémuriens, autres mammifères, reptiles et amphibiens, poissons d'eau douce et evaluation de la viabilité des populations et des habitats (PHVA) de *Hypogeomys antimena* (Vositse). Appel Valley, Minnesota: CBSG.

Cooper, N., Rodriguez, J., and Purvis, A. (2008). A common tendency for phylogenetic overdispersion in mammalian assemblages. Proceedings of the Royal Society B, Biological Sciences. 275(1646), 2031-2037.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G., Poorter, H. (2003). A handbook of protocols for standarised and easy measurement of plant functional traits worldwide. Australian Journal of Botany. 51, 335-380.

Cornwell, W.K., and Ackerly D.D. (2009). Community assembly and shifts in the distribution of trait values across an environmental gradient in coastal California. Ecological Monographs. 79, 109-126.

Cornwell, W.K., D.W. Schwilk, and Ackerly, D. D. (2006). A trait-based test for habitat filtering, convex hull volume. Ecology. 87, 1465-1471.

Cortes-Ortiz, L., Bermingham, E., Rico, C., Rodriguez-Luna, E., Sampaio, I., and Ruiz-Garcia, M. (2003). Molecular systematics and biogeography of the Neotropical monkey genus, *Alouatta*. Molecular Phylogenetics and Evolution. 26(1), 64-81.

Cottenie, K. (2005). Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters. 8(11), 1175-1182.

Cowlishaw, G. (1999). Predicting the pattern of decline of African primate diversity, an extinction debt from historical deforestation. Conservation Biology. 13, 1183-1193.

Craul, M., Zimmerman, E., Rasoloharijaona, S., Randrianambinina, B., and Radespiel, U. (2007). Unexpected species diversity of Malagasy primates (*Lepilemur* spp.) in the same biogeographical zone, a morphological and molecular approach with the description of two new species. BMC Evolutionary Biology. 7, 15.

Cronin, L. (2008). *Australian Mammals*. Australia: Allen & Unwin.

Crowley, B.E. (2010). A refined chronology of prehistoric Madagascar and the demise of the megafauna. Quaternary Science Reviews. 29, 2591-2603.

Dammhahn, M., Soarimalala, V., and Goodman, S.M. (2013). Trophic niche differentiation and microhabitat utilization in a species-rich montane forest small mammal community of Eastern Madagascar. Biotropica. 45(1), 111-118.

Darwin, C.R. (1859). *On The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray.

Dausmann, K.H., Glos, J., Ganzhorn, J.U., and Heldmaier, G. (2004). Hibernation in a tropical primate. Nature. 429, 825-826.

Davies, T.J., Fritz, S.A., Grenyer, R., Orme, C.D.L., Bielby, J., Bininda- Emonds, O.R.P., Cardillo, M., Jones, K. E., Gittleman, J. L., Mace, G. M., and Purvis, A. (2008). Phylogenetic trees and the future of mammalian biodiversity. Proceedings of the National Academy of Sciences, USA. 105, 11556-11563.

Dawson T.J., and Fanning, F.D. (1981). Thermal and energetic problems of semiaquatic mammals: a study of the Australian water-rat, including comparisons with the platypus. Physiological Zoology. 54, 285-296.

Dayan, T., and Simberloff, D. (1994). Character displacement, sexual size dimorphism, and morphological variation among the mustelids of the British Isles. Ecology. 75, 1063-1073.

de Bello, F., Leps, J., and Sebastia, M.-T. (2005). Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. Journal of Applied Ecology. 42, 824-833.

de Wit, M.J. (2003). Madagascar, heads it's a continent, tails it's an island. *Annual Review of Earth and Planetary Sciences, 31*(1), 213-248.

Department of the Environment (2015). *Community and Species Profile and Threats Database*, Department of the Environment, Canberra. Available from: http://www.environment.gov.au/sprat.

DeFries, R., Hansen, A., Newton, A.C., and Hansen, M.C. (2005). Increasing isolation of protected areas in tropical forests over the past twenty years. Ecological Applications. 15(1), 19-26.

Devictor, V., Whittaker, R.J., and Beltrame, C (2010). Beyond scarcity, citizen science programmes as useful tools for conservation biogeography. Diversity and Distributions. 16(3), 354-362.

Dewar, R. E., and Richard, A. F. (2007). Evolution in the hypervariable environment of Madagascar. Proceedings of the National Academy of Science USA. 104, 13723-13727.

Dexter, K.G., Terborgh, J.W., and Cunningham, C.W. (2012). Historical effects on beta diversity and community assembly in Amazonian trees. Proceedings of the National Academy of Sciences, 109(20), 7787-7792.

Diamond, J.M. (1975). Assembly of species communities. In M.L. Cody and J.M. Diamond (Eds.). *Ecology and Evolution of Communities* (Pp. 342-444). Cambridge: Harvard University Press.

Diaz, S., and Cabido, M. (1997). Plant functional types and ecosystem function in relation to global change, a multiscale approach. Journal of Vegetation Science. 8, 463-474.

Diaz, S., and M. Cabido. (2001). Vive la difference, Plant functional diversity matters to ecosystem processes. Trends in Ecology and Evolution. 16, 646-655.

Diaz, S., Cabido, M., Casanoves, F. (1999). Functional implications of trait-environment linkages in plant communities. In E. Weiher and P. Keddy (Eds.). *Ecological Assembly Rules, Perspectives, Advances, Retreats* (Pp. 338-362). Cambridge, UK: Cambridge University Press.

Diaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., and Robson, M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. Proceedings of the National Academy of Sciences. 104, 20684-20689.

Di Fiore, A., and Rendall, D. (1994). Evolution of social organization: a reappraisal for primates by using phylogenetic methods. Proceedings of the National Academy of Science. 91, 9941–-9945.

Dineen, A.A., Fraiser, M.L., and Sheehan, P.M. (2014). Quantifying functional diversity in pre- and post-extinction paleocommunities, a test of ecological restructuring after the end-Permian mass extinction. Earth-Science Reviews. 136, 339-349.

Diniz-Filho, J.A.F., Bini, L.M., and Hawkins, B.A. (2003). Spatial autocorrelation and red herrings in geographical ecology. Global Ecology and Biogeography. 12, 53-64.

Dollar, L.J. (1999). Notice of *Eupleres goudotii* in the rain forest of south eastern Madagascar. Small Carnivore Conservation. 20, 30-31.

Dollar, L.J. (2006). *Morphometrics, diet and conservation of Cryptoprocta ferox*. PhD dissertation, Duke University. Durham, North Carolina: ProQuest/UMI. (Publication No. 3267903.)

Donati, G., Santini, L., Razafindramanana, J., Boitani, L., and Borgognini-Tarli, S. (2013). (Un-).expected nocturnal activity in "diurnal" *Lemur catta* supports cathemerality as one of the key adaptations of the lemurid radiation. American Journal of Physical Anthropology. 150(1), 99-106.

Donque, G. (1972). The climatology of Madagascar. In R. Battistini and G. Richard-Vindard (Eds.). *Biogeography and Ecology in Madagascar* (Pp. 87-144). The Hague: Kluwer Academic Publishers.

Donque, G., (1975). *Contribution géographique à l'étude du climat de Madagascar*. Antananarivo: Nouvelle Imprimerie des Arts Graphiques.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M., and Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data, a review. Ecography. 30(5), 609-628.

Dornelas, M., Connolly, S.R., and Hughes, T.P. (2006). Coral reef diversity refutes the neutral theory of biodiversity. Nature. 440, 80-82.

Dray, S., Legendre, P., and Blanchet, G. (2011). Packfor, Forward selection with permutation (Canoco p.46). R package version 0.0-8/r100. http://R-Forge.R-project.org/projects/sedar/

Dray, S., Pélissier, R., Couteron, P., and Fortin, M. (2012). Community ecology in the age of multivariate multiscale spatial analysis. Ecological Monographs. 82(3), 257-275.

Dray, S., Legendre, P., and Peres-Neto, P.R. (2006). Spatial modelling, a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling. 196(3-4), 483-493.

Duarte, L.S. (2011). Phylogenetic habitat filtering influences forest nucleation in grasslands. Oikos. 120(2), 208-215.

Duckworth, J.W., and Rakotondraparany, F. (1990). The mammals of Marojejy. International Council for Bird Preservation Study Report. 40, 54-60.

Dunning, J.B., Danielson, J.B., Pulliam, H.R. (1992). Ecological processes that affect populations in complex landscapes. Oikos. 65, 169-175.

Eiserhardt, W.L., Svenning, J.-C., Baker, W.J., Couvreur, T.L.P., and Balslev, H. (2013). Dispersal and niche evolution jointly shape the geographic turnover of phylogenetic clades across continents. Scientific Reports. 3, 1164.

Ejrnæs, R., Bruun, H.H., and Graae, B.J. (2006). Community assembly in experimental grasslands, suitable environment or timely arrival? Ecology. 87(5). 1225-1233.

Eldridge, M.D.B. (2012). Purple-necked rock-wallaby, *Petrogale purpureicollis*. In L.K. Curtis, A.J. Dennis, K.R. McDonald, P.M. Kyne and S.J.S. Debus (Eds.) *Queensland's Threatened Animals* (Pp. 362-363). Collingwood: CSIRO Publishing.

Eldridge, M.D.B., Johnson, P.M., Hensler, P., Holden, J.K., and Close, R.L. (2008). Distribution of three parapatric cryptic species of rock-wallaby (*Petrogale*) in north-east Queensland: *P. assimilis*, *P. mareeba* and *P. sharmani*. Australian Mammalogy. 30(1), 37-42.

Eldgride, M.D.B., Wilson, A.C.C., Metcalfe, C.J., Dolling, A.E., Bell, J.N., Johnson, P.M., Johnston, P.G., and Close, R.L. (2001). Taxonomy of rock wallabies, *Petrogale* (Marsupialia: Macropodidae). III. Molecular data confirms the species status of the purple-necked rock-wallaby *Petrogale purpureicollis* Le Souef 1924. Australian Journal of Zoology. 49, 323-343.

Elith, J., and Leathwick, J.R. (2009). Species distribution models, ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics. 40(1), 677-697.

Ellis, B.A., Tierney, P.J., and Dawson, T.J. (1992). The diet of the Bridled Nailtail Wallaby (*Onychogalea fraenanta*). I. Site and seasonal influence and dietary overlap with the Black-striped Wallaby (*Macropus dorsalis*) and domestic cattle. Wildlife Research. 19, 65-78.

Ellis, W., Melzer, A., Bercovitch, F.B. (2009). Spatiotemporal dynamics of habitat use by koalas: the checkerboard model. Behavioral Ecology and Sociobiology. 63(8), 1181-1188.

Emerson, B.C., and Gillespie, R.G. (2008). Phylogenetic analysis of community assembly and structure over space and time. Trends In Ecology and Evolution. 23(11), 619-630.

Emerson, B.C., Cicconardi, F., Fanciulli, P.P., and Shaw, P.J.A (2011). Phylogeny, phylogeography, phylobetadiversity and the molecular analysis of biological communities. Philosophical Transactions of The Royal Society B, Biological Sciences. 366(1576), 2391-2402.

Emmons, L.H., Gautier-Hion, A., and Dubost, G. (1983). Community structure of the frugivorous-folivorous forest mammals of Gabon. Journal of Zoology. 199, 209-222.

Emmons, L.H. (1984). Geographic variation in densities and diversities of non-flying Amazonian mammals. Biotropica. 16, 210-222.

Esselstyn, J.A., Maher, S.P., and Brown, R.M. (2011). Species interactions during diversification and community assembly in an island radiation of shrews. PLOS ONE. 6(7), e21885.

Ezcurra, M.D., and Agnolin, F.L. (2012). A new global palaeobiogeographical model for the late Mesozoic and early Tertiary. Systematic Biology. 61(4), 553-566.

Faith, D. (1992). Conservation evaluation and phylogenetic diversity. Biological Conservation. 61, 1-10.

Fauth, J.E., Bernardo, J., Camara, M., Resetarits, W.J.Jr., Van Buskirk, J., and McCollum, S.A. (1996). Simplifying the jargon of community ecology, a conceptual approach. The American Naturalist. 147(2), 282-286.

Feistner, A.T.C., and Schmid, J. (1999). Lemurs of the Réserve Naturelle Intégrale d'Andohahela, Madagascar. A Floral and Faunal Inventory of the of the Réserve Naturelle Intégrale d'Andohahela, Madagascar, with reference to elevational variation. Fieldiana. 94, 269-283.

Fimbel, R.A., Grajal, A., Robinson, J.G. (2011). *The Cutting Edge: Conserving Wildlife in Logged Tropical Forest*. New York: Columbia University Press.

Firth, R.S.C., Jefferys, E., Woinarski, J.C.Z., and Noske, R.A. (2005). The diet of the brush-tailed rabbit-rat (*Conilurus penicillatus*) from the monsoonal tropics of the Northern Territory, Australia. Wildlife Research. 32, 517-523.

Fischer, D., Moeller, P., Thomas, S.M., Naucke, T.J., and Beierkuhnlein, C. (2011). Combining climatic projections and dispersal ability: a method for estimating the responses of sandfly vector species to climate change. PLoS Neglected Tropical Diseases, 5(11), e1407.

Fisher, C.K., and Mehta, P. (2014). The transition between the niche and neutral regimes in ecology. Proceedings of the National Acedemy of Science. 111(36), 13111-13116.

Fisher, D.O., Blomberg, S.P., and Owens, I.P.F (2003). Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. Proceedings of The Royal Society B, Biological Sciences. 270(1526), 1801-1808.

FitzJohn, R.G. (2010). Quantitative traits and diversification. Systematic Biology. 59 (6), 619-633.

Flannery, T. (1990a). Pleistocene faunal loss, implications of the aftershock for Australia's past and future. Archaeology in Oceania. 25, 45-67.

Flannery, T. (1990b). *The Australian Museum Mammals of New Guinea*. Australia: Robert Brown & Associates.

Flannery, T. (1995). *Mammals of New Guinea*. Ithaca: Cornell Unversity Press.

Fleagle, J.G. (1999). *Primate Adaptation and Evolution.* San Diego: Academic Press.

Fleagle, J.G., Janson, C., and Reed, K.E. (1999). *Primate Communities*. Cambridge: Cambridge Unviersity Press.

Fleagle, J.G., and Reed, K.E. (1999). Phylogenetic and temporal perspectives on primate ecology. In JG Fleagle, C Janson, KE Reed (Eds.). *Primate Communities* (Pp. 92-115). New York, NY: Cambridge University Press.

Flynn, D.F.B., Mirotchnick, N., Jain, M., Palmer, M.I., and Naeem, S. (2011). Functional and phylogenetic diversity as predictors of biodiversity-ecosystem-function relationships. Ecology. 92, 1573-1581.

Folmer, H., and Oud, J. (2008). How to get rid of W: a latent variables approach to modelling spatially lagged variables. Environment and Planning A. 40(10), 2526-2538.

Fooden J. (1972). Breakup of Pangea and isolation of relict mammals in Australia, South America, and Madagascar. Science. 175, 894-898.

Fortin, M.-J., and Dale, M.R.T. (2005). *Spatial analysis, a guide for ecologists*. Cambridge: Cambridge University Press.

Fox, B.J. (1987). Species assembly and the evolution of community structure. Evolutionary Ecology. 1, 201-213.

Fox, B.J. (1999). The genesis and development of guild assembly rules. In, Weiher, E., and Keddy, P. (Eds.). *Ecological Assembly Rules, Perspectives, Advances, Retreats* (Pp. 23-57). Cambridge: Cambridge University Press.

Fox, B.J. (1984). The diets of *Sminthopsis murina* and *Antechinus stuartii* (Marsupialia: Dasyuridae) in sympatry. Australian Wildlife Research. 11, 235-248.

Fox, B.J., and Brown, J.H. (1993). Assembly rules for functional groups in North American desert rodent communities. Oikos. 67, 358-370.

Fox, B.J., and Fox, M.D. (2000). Factors determining mammal species richness on habitat islands and isolates, habitat diversity, disturbance, species interactions and guild assembly rules. Global Ecology and Biogeography. 9(1), 19-37.

Fox, B.J., and Kirkland, G.L. (1992). An assembly rule for functional-groups applied to north-american soricid communities. Journal of Mammology. 73, 491-503.

Freed, B.Z. (1996). *Co-occurrence among crowned lemurs (Lemur coronatus) and Sanford's lemurs (Lemur fulvus sanfordi) of Madagascar*. PhD dissertation, Washington University. Saint Louis.

Freestone, A.L., and Inouye, B.D. (2006). Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. Ecology. 87, 2425-2432.

Fritz, S.A., Bininda-Emonds, O.R.P., and Purvis, A. (2009). Geographical variation in predictors of mammalian extinction risk, big is bad, but only in the tropics. Ecology Letters. 12, 538-549.

Fryxell, J.M., Falls, J.B., Falls, E.A., and Brooks, R.J. (1998). Long-term dynamics of small mammal populations in Ontario. Ecology. 79, 213-225.

Fukami, T., Bezemer, T.M., Mortimer, S.R., and van der Putten, W.H. (2005). Species divergence and trait convergence in experimental plant community assembly. Ecology Letters. 8, 1283-1290.

Ganzhorn, J.U. (1987). A possible role of plantations for primate conservation in Madagascar. American Journal of Primatology. 12(2), 205-215.

Ganzhorn, J.U. (1988). Food partitioning among Malagasy primates. Oecologia. 75, 436-450.

Ganzhorn, J.U. (1995). Low level forest disturbance effects on primary production, leaf chemistry, and lemur populations. Ecology. 76, 2084-2096.

Ganzhorn, J.U. (1997). Test of Fox's assembly rule for functional groups in lemur communities in Madagascar. Journal of Zoology. 241, 533-542.

Ganzhorn, J.U. (1998). Nested patterns of species composition and their implications for lemur biogeography in Madagascar. Folia Primatologica. 69, 332-341.

Ganzhorn, J.U. (1999). Body mass, competition and the structure of primate communities. In J.G. Fleagle, C.H. Janson and K.E. Reed (Eds.). *Primate Communities* (Pp. 141-157). Cambridge: Cambridge University Press.

Ganzhorn, J.U., Malcomber, S., and Andrianantoanina, O. (1997). Habitat characteristics and lemur species richness in Madagascar. Biotropica. 29(3), 331-343.

Ganzhorn, J.U., Goodman, S.M., Nash, S., and Thalmann, U. (2006). Lemur biogeography. In J.G. Fleagle and S. Lehman (Eds.). *Primate Biogeography* (Pp. 229-254). Cambridge: Cambridge University Press.

Ganzhorn, J.U., Sommer, S., Abraham, J., Ade, M., Raharivololona, B.M., Rakotovao, E.R., Rakotondrasoa, C., and Randriamarosoa, R. (1996). Mammals of the Kirindy Forest with special emphasis on *Hypogeomys antimena* and the effects of logging on the small mammal fauna. Primate Report. 46, 215-232.

Ganzhorn, J.U., and Sorg, J.-P. (1996). Ecology and economy of a tropical dry forest. Primate Report. 83(2), 46-1.

Ganzhorn, J.U., Wilmé, L., and Mercier, J.-L. (2014). Explaining Madagascar's. biodiversity. In Scales, I.R. (Ed.). *Conservation and Environmental Management in Madagascar* (Pp. 17-43). New York: Routledge.

Ganzhorn, J.U., Wright P.C., and Ratsimbazafy, J. (1999). Primate communities, Madagascar. In, Fleagle, J.F., Janson, C., and Reed, K. (Eds.). *Primate Communities* (Pp. 75-89). Cambridge: Cambridge University Press.

Garbutt, N. (2007). *Mammals of Madagascar - A Complete Guide*. London: Yale University Press.

García, D., Zamora, R., and Amico, G.C. (2010). The spatial scale of plant-animal interactions, effects of resource availability and habitat structure. Ecological Monographs. 81(1), 103-121.

Gause, G.F. (1934). The struggle for existence. Baltimore, MD: Williams and Wilkins.

Gautier-Hion, A., Emmons. L.H., and Dubost, G. (1980). A comparison of the diets of three major groups of primary consumers of Gabon (primates, squirrels and ruminants). Oecologia. 45, 182-189.

Gavilanez, M.M., and Stevens, R.D. (2013). Role of environmental, historical and spatial processes in the structure of Neotropical primate communities, contrasting taxonomic and phylogenetic perspectives. Global Ecology and Biogeography. 22(5), 607-619.

Geiser, F. (1994). Hibernation and daily torpor in marsupials, a review. Australian Journal of Zoology. 42, 1-16.

Geiser, F. (2004). Metabolic rate and body temperature reduction during hibernation and daily torpor. Annual Review Physiology. 66, 239-274.

Geiser, F., and Baudinette, R.V. (1987). Seasonality of torpor and thermoregulation in three dasyurid marsupials. Journal of Comparative Physiology B. 153(3), 335-344.

Geiser, F., and Turbill, C. (2009). Hibernation and daily torpor minimize mammalian extinctions. Naturwissenchaften. 96, 1235-1240.

Genin, F., and Perret, M. (2003). Daily hypothermia in captive grey mouse lemurs (*Microcebus murinus*), effects of photoperiod and food restriction. Comparative Biochemistry and Physiology B. 136, 71-81.

Gerber, B.D. (2010). Madagascar Protected Areas. Madagascar GIS. Retrieved, June 15 2012. http://filebox.vt.edu/users/bgerber/services.htm

Gerber, B. D., Karpanty, S.M., and Randrianantenaina, J. (2012). Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence. Journal of Mammology. 93(3), 667-676.

Gering, J.C., and Crist, T.O. (2002). The alpha-beta-regional relationship, providing new insights into local-regional patterns of species richness and scale dependence of diversity components. Ecology Letters. 5(3), 433-444.

Gilbert, B., and Lechowicz, M.J. (2004). Neutrality, niches, and dispersal in a temperate forest understory. Proceedings of the National Academy of Sciences. 101(20), 7651-7656.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W., and Holt, R.D. (2010). A framework for community interactions under climate change. Trends in Ecology and Evolution. 25(6), 325-331.

Gleason, H (1926). The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club. 53(1), 7-26.

Glen, A.S., and Dickman, C.R. (2008), Niche overlap between marsupial and eutherian carnivores: does competition threaten the endangered spotted-tailed quoll? Journal of Applied Ecology. 45(2), 700-707.

Godfrey, L.R., Jungers, W.L., Reed, K.E., Simons, L., and Chatrath, P.S. (1997). Subfossil lemurs: Inferences about past and present primate communities. In S.M. Goodman and B.D. Patterson (Eds.). *Natural Change and Human Impact in Madagascar* (Pp. 218–256). Washington, DC: Smithsonian Institution Press.

Godfrey, L.R., Jungers, W.L., Simons, E.L., Chatrath, P.S., and Rakotosamimanana, B. (1999). Past and present distributions of lemurs in Madagascar. In Rakotosamimanana, B., Rasamimanana, H., Ganzhorn, J. U., and Goodman, S. M. (Eds.). *New Directions in Lemur Studies* (Pp. 19–53). New York: Kluwer Academic/Plenum.

Gómez, J.M., and Verdú, M. (2012). Mutualism with plants drives primate diversification. Systematic Biology. 61(4), 567-577.

Gongora, J., Swan, A.B., Chong, A.Y., Ho, S.Y.W., Damayanti, C.S., Kolomyjec, S., Gust, N. (2012). Genetic structure and phylogeography of platypuses revealed by mitochondrial DNA. Journal of Zoology. 286(2), 110-119

González-Megías, A., Gómez, J.M., and Sánchez-Piñero, F. (2005). Consequences of spatial autocorrelation for the analysis of metapopulation dynamics. Ecology. 86(12), 3264-3271.

Goodman, S.M. (1996). A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar, with reference to elevational variation. Fieldiana. 85, 1-319.

Goodman, S.M. (1998). A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar, with reference to elevational variation. Fieldiana. 90, 1-246.

Goodman, S.M. (1999). A floral and faunal inventory of the of the Réserve Naturelle Intégrale d'Andohahela, Madagascar, with reference to elevational variation. Fieldiana. 94, 1-297.

Goodman, S.M. (2000). A floral and faunal inventory of the Parc National de Marojejy, Madagascar, with reference to elevational variation. Fieldiana. 97, 1-286.

Goodman, S.M. (2003a). *Oryzorictes*, mole tenrec or rice tenrec. In S.M. Goodman, and J.P. Benstead (Eds.). *The Natural History of Madagascar* (Pp. 1278-1281). Chicago: The University of Chicago Press.

Goodman, S.M. (2003b). *Galidia elegans*, ring-tailed mongoose. In S.M. Goodman and J.P. Benstead (Eds.). *The Natural History of Madagascar* (Pp. 1351-1354). Chicago: The University of Chicago Press.

Goodman, S.M., Andrianarimisa, A., Olson, L.E., and Soarimalala, V. (1996). Patterns of elevational distribution of birds and small mammals in the humid forests of Montagne d'Ambre, Madagascar. Ecotropica. 2, 87-98.

Goodman, S.M., and Benstead, J.P. (2003). *The Natural History of Madagascar*. Chicago: University of Chicago Press.

Goodman, S.M., and Benstead, J.P. (2005). Updated estimates of biotic diversity and endemism for Madagascar. Oryx. 39, 73-77.

Goodman, S.M., and Carleton, M.D. (1996). The rodents of the Reserve Naturelle Integrale d'Andringitra, Madagascar, with reference to elevational variation. Fieldiana. 85, 257-283.

Goodman, S.M., and Carleton, M.D. (1998). The rodents of the Reserve Speciale d'Anjanharibe-Sud, Madagascar. Fieldiana. 90, 201-221.

Goodman, S. M., Carleton, M. D., and Pidgeon, M. (1999). The rodents of the Reserve Naturelle Integrale d'Andohahela, Madagascar. Fieldiana. 64, 217-249.

Goodman, S. M., and Ganzhorn, J. U. (2004a). Biogeography of lemurs in the humid forests of Madagascar, the role of elevational distribution and rivers. Journal of Biogeography. 31(1), 47-55.

Goodman, S., and Ganzhorn, J. (2004b). Elevational ranges of lemurs in the humid forests of Madagascar. International Journal of Primatology. 25(2), 331-350.

Goodman, S.M., Ganzhorn, J.U., Olson, L.E., Pidgeon, M., and Soarimalala, V. (1997a). Annual variation in species diversity and relative density of rodents and insectivores in the Parc National de la Montagne d'Ambre, Madagascar. Ecotropica. 3, 109-118.

Goodman, S.M., Ganzhorn, J.U., and Rakotondravony, D. (2003a). Introduction to the mammals. In S.M. Goodman, and J.P. Benstead (Eds.). *The Natural History of Madagascar* (Pp. 1159-1190). Chicago: The University of Chicago Press.

Goodman, S.M., and Jenkins, P.D. (1998). The insectivores of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar. A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar, with reference to elevational variation. Fieldiana. 90, 139-161.

Goodman, S.M., Jenkins, P., and Pidgeon, M. (1999). The Lipotyphla (Tenrecidae and Soricidae) of the Reserve Naturelle Integrale d'Andohahela, Madagascar. Fieldiana. 94, 187-216.

Goodman, S.M.and Jenkins, P.D. (2000). Tenrecs (Lipotyphla, Tenrecidae). of the Parc National de Marojejy, Madagascar. A floral and faunal inventory of the Parc National de Marojejy, Madagascar, with reference to elevational variation. Fieldiana. 97, 201-229.

Goodman, S.M., Kerridge, F.J., and Ralisoamalala, R.C. (2003b). A note on the diet of *Fossa fossana* (Carnivora). in the central eastern humid forests of Madagascar. Mammalia. 67, 595-598.

Goodman, S.M., Langrand, O., and Rasolonandrasana, B.P.N. (1997b). The food habits of *Cryptoprocta ferox* in the high mountain zone of the Andringitra Massif, Madagascar (Carnivora, Viverridae). Mammalia. 61, 185-192.

Goodman, S.M., and Langrand, O. (1994). *Inventaire Biologique Forêt de Zombitse. Recherches pour le Développement*, *Série Sciences Biologiques, No. Spéciale*. Antananarivo: Centre d'Information et de Documentation Scientifique et Technique.

Goodman, S.M., Raheriarisena, M., and Jansa, S.A. (2009). A new species of *Eliurus* Milne Edwards, 1885 (Rodentia, Nesomyinae). from the Réserve Spéciale d'Ankarana, northern Madagascar. Bonner zoologische Beiträge. 56,133-149.

Goodman, S.M., Raherilalao, M.J., Rakotomalala, D., Rakotondravony, D., Raselimanana, A.P., Razakarivony, H.V., and Soarimalala, V. (2002). Inventaire des vertebres du Parc National de Tsimanampetsotsa (Toliara). Akon'ny Ala. 28, 1-36.

Goodman, S.M., and Rakotondravony, D. (2000). The effects of forest fragmentation and isolation on insectivorous small mammals (Lipotyphla) on the Central High Plateau of Madagascar. Journal of Zoology. 250, 193-200.

Goodman, S.M., Rakotondravony, D., Randriamanantsoa, H.N., and Rakotomalala-Razanahoera, M. (2005). A new species of rodent from the montane forest of central eastern Madagascar (Muridae, Nesomyinae, *Voalavo*). Proceedings of the Biological Society of Washington. 118, 863-873.

Goodman, S.M., and Raselimanana, A.P. (2002). The occurrence of Allocebus trichotus in the Parc National de Marojejy. Lemur News. 7, 21-22.

Goodman, S.M., and Rasolonandrasana, B.P.N. (1999). *Inventaire biologique de la Réserve Spéciale du pic d'Ivohibe et du couloir forestier qui la relie au Parc National d'Andringitra. Recherches pour le Développement, Série Sciences Biologiques No. 15*. Antananarivo: Centre d'Information et de Documentation Scientifique et Technique.

Goodman, S.M., and Rasolonandrasana, B.P.N. (2001). Elevational zonation of birds, insectivores, rodents and primates on the slopes of the Andringitra Massif, Madagascar. Journal of Natural History. 35, 285-305.

Goodman, S.M, Raxworthy, C.J., Maminirina, C.P., and Olson, L.E. (2006). A new species of shrew tenrec (*Microgale jobihely*) from northern Madagascar. Journal of Zoology. 270, 384-398.

Goodman, S.M., and Razafindratsita, V.R. (2001). *Inventaire biologique du Parc National de Ranomafana et du couloir forestier qui la relie au Parc National d'Andringitra, Recherches pour le Développement, Série Sciences Biologiques No. 17*. Antananarivo: Centre d'Information et de Documentation Scientifique et Technique. .

Goodman, S.M., and Schütz, H. (1999). Observations of lemurs in the forest east of Tsinjoarivo, Ambatolampy. Lemur News. 4, 14-16.

Goodman, S.M., and Soarimalala, V. (2002). Les petits mammifères de la Réserve Spéciale de Manongarivo, Madagascar. Inventaire biologique de la réserve spéciale de Manongarivo (NW Madagascar). Boissiera. 59, 359-383.

Goodman, S.M., and Soarimalala, V. (2004). A new species of *Microgale* (Lipotyphla, Tenrecidae, Oryzorictinae) from the Forêt des Mikea of southwestern Madagascar. Proceedings of the Biological Society of Washington. 117, 251-265.

Goodman, S.M., and Soarimalala, V. (2005). A new species of *Macrotarsomys* (Rodentia, Muridae, Nesomyinae) from southwestern Madagascar. Proceedings of the Biological Society of Washington. 118, 450-464.

Goodman, S.M., and Wilmé, L. (2003). *Nouveaux résultats d'inventaires biologiques faisant référence à l'altitude dans la région des massifs montagneux de Marojejy*

et d'Anjanaharibe-Sud. Recherches pour le Développement, Série Sciences Biologiques No. 19. Antananarivo: Centre d'Information et de Documentation Scientifique et Technique.

Goodman, S.M., and Wilmé, L. (2006). *Inventaires de la faune et de la flore du nord de Madagascar dans la région Loky-Manambato, Analamerana et Andavakoera. Recherches pour le Développement, Série Sciences Biologiques No. 23*. Antananarivo: Centre d'Information et de Documentation Scientifique et Technique.

Gordon A.D., Johnson S.E., and Louis Jr. E.E. (2013). Females are the ecological sex, Sex-specific body mass ecogeography in wild sifaka populations (*Propithecus* spp.). American Journal of Physical Anthropology. 151, 77-87.

Gower, J.C. (1971). A General Coefficient of Similarity and Some of its Properties. Biometrics. 27, 857-871.

Grace, J.B. (2006). *Structural Equation Modeling and Natural Systems*. Cambridge: Cambridge University Press.

Grace, J.B., Anderson, T.M., Olff, H., and Scheiner, S.M. (2010). On the specification of structural equation models for ecological systems. Ecological Monographs. 80, 67-87.

Graham, C.H., and Fine, P.V.A. (2008). Phylogenetic beta diversity, linking ecological and evolutionary processes across space in time. Ecology Letters. 11, 1265-1277.

Graham, C.H., Parra, J.L., Rahbek, C., and McGuire, J.A. (2009). Phylogenetic structure in tropical hummingbird communities. Proceedings of the National Academy of Science. 106, 673-678.

Grassi, C. (2006). Variability in habitat, diet, and social structure of *Hapalemur griseus* in Ranomafana National Park, Madagascar. American Journal of Physical Anthropology. 131, 50-63.

Gravel, D., Canham, C. D., Beaudet, M., and Messier, C. (2006). Reconciling niche and neutrality, the continuum hypothesis. Ecology Letters. 9(4), 399-409.

Griffin, R.H., Matthews, L.J., Nunn, C.L. (2012). Evolutionary disequilibrium and activity period in primates: a Bayesian phylogenetic approach. American Journal of Physical Anthropology. 147, 409-416.

Griffith, D.A., and Peres-Neto, P.R. (2006). Spatial modeling in ecology, the flexibility of eigenfunction spatial analyses. Ecology. 87(10), 2603-2613.

Grigg, G., Beard, L., Grant, T., Augee, M. (1992). Body temperature and diurnal activity patterns in the platypus (*Ornithorhynchus anatinus*) during Winter. Australian Journal of Zoology. 40, 135-142.

Grime, J.P. (2002). Declining plant diversity: empty niches or functional shifts? Journal of Vegetation Science. 13(4), 457-460.

Grime, J.P. (2006). Trait convergence and trait divergence in herbaceous plant communities, mechanisms and consequences. Journal of Vegetation Science. 17, 255-260.

Grinnel, J. (1917). The niche-relationships of the California Thrasher. The Auk. 34, 427-433.

Hanna, E., and Cardillo, M. (2014). Clarifying the relationship between torpor and anthropogenic extinction risk in mammals. Journal of Zoology. 293(3., 211-217.

Hanya, G., and Aiba, S. (2010). Fruit fall in tropical and temperate forests, implications for frugivore diversity. Ecological Research. 25, 1081-1090.

Hanya, G., Stevenson, P., van Noordwijk, M., Wong, S.T., Kanamori, T., Kuze, N., Aiba, S., Chapman, C.A., and van Schaik, C. (2011). Seasonality in fruit availability affects frugivorous primate biomass and species richness. Ecography. 34, 1009-1017.

Harcourt, A.H., and Wood, M.A. (2012). Rivers as barriers to primate distributions in Africa. International Journal of Primatology. 33(1), 168-183.

Hardy, O.J., and Senterre, B. (2007). Characterizing the phylogenetic structure of communities by an additive partitioning of phylogenetic diversity. Journal of Ecology. 95, 493-506.

Harper, G.J., Steininger, M.K., Tucker, C.J., Juhn, D., and Hawkins, F. (2007). Fifty years of deforestation and forest fragmentation in Madagascar. Environmental Conservation. 34(4), 325-333.

Harpole, W.S. and Tilman, D. (2006). Non-neutral patterns of species abundance and species traits. Ecology Letters. 9, 15-23.

Harris, D. (2009). Review of negative effects of introduced rodents on small mammals on islands. Biological Invasions. 11(7), 1611-1630.

Harrison, S., and Cornell, H. (2008). Toward a better understanding of the regional causes of local community richness. Ecology Letters. 11(9), 969-979.

Hawes, J.E., and Peres, C.A. (2014). Ecological correlates of trophic status and frugivory in neotropical primates. Oikos. 123(3), 365-377.

Hawkins, A.F.A. (1994). *Eupleres goudotii* in west Malagasy deciduous forest. Small Carnivore Conservation. 20, 30-31.

Hawkins, A.F.A. (1999). The primates of Isalo National Park, Madagascar. Lemur News. 4, 10-14.

Hawkins, A.F.A., Chapman, P., Ganzhorn, J.U., Bloxam, Q.M.C., Barlow, S.C., and Tonge, S.J. (1990). Vertebrate conservation in Ankarana Special Reserve, Northern Madagascar. Biological Conservation. 54, 83-110.

Hawkins, B.A., and Porter, E.E. (2003). Does herbivore diversity depend on plant diversity? The case of California butterflies. The American Naturalist. 161, 40-49.

Hawkins, C.E. (2003). *Cryptoprocta ferox*, fossa, fosa. In S.M. Goodman and J.P. Benstead (Eds.). *The Natural History of Madagascar* (Pp. 1360-1363). Chicago: The University of Chicago Press.

Hawkins, C.E., and Racey, P.A. (2008). Food habits of an endangered carnivore, *Cryptoprocta ferox*, in the dry deciduous forests of western Madagascar. Journal of Mammalogy. 89, 64-74.

Hayes, J.P., and Jenkins, S.H. (1997). Individual variation in mammals. Journal of Mammology. 78, 274-293.

He, F., Gaston, K., Connor, E., and Srivastava, D. (2005). The local-regional relationship, immigration, extinction, and scale. Ecology. 86(2), 360-365.

He, K., and Zhang, J. (2009). Testing the correlation between beta diversity and differences in productivity among global ecoregions, biomes, and biogeographical realms. Ecological Informatics. 4(2), 93-98.

Heckman, K.L., Rasoazanabary, E., Machlin, E., Godfrey, L.R., and Yoder, A.D. (2006). Incongruence between genetic and morphological diversity in *Microcebus griseorufus* of Beza Mahafaly. BMC Evolutionary Biology. 6, 98. doi:10.1186/1471-2148-6-98

Hein, A., and Gillooly, J. (2011). Predators, prey, and transient states in the assembly of spatially structured communities. Ecology. 92(3), 549-555.

Heino J., Bini L., Karjalainen S., Mykrä H., Soininen J., Vieira L., and Diniz-Filho J. (2010). Geographical patterns of micro-organismal community structure, are diatoms ubiquitously distributed across boreal streams? Oikos. 119, 129-137.

Helmus, M.B.T., Williams, C., and Ives, A. (2007). Phylogenetic measures of biodiversity. The American Naturalist. 169(3), E68-E83.

Helmus, M.B.T, Savage, K., Diebel, M., and Maxted, J. (2007). Separating the determinants of phylogenetic community structure. Ecology. 10, 917-925.

Hemingway, C.A. (1995). *Feeding and reproductive strategies of Propithecus diadema edwardsi.* PhD dissertation, Duke University. Durham, North Carolina.

Hérault, B. (2007). Reconciling niche and neutrality through the Emergent Group approach. Perspectives in Plant Ecology, Evolution and Systematics. 9(2), 71-78.

Herrera, C.M. (2002). Seed dispersal by vertebrates. In C.M. Herrera and O. Pellmyr (Eds.). *Plant-Animal Interactions. An Evolutionary Approach* (Pp. 185-208). Oxford: Blackwell Science.

Hickerson, M.J., Carstens, B.C., Cavender-Bares, J., Crandall, K.A., Graham, C.H., Johnson, J.B., Yoder, A.D. (2010). Phylogeography's past, present, and future, 10 years after. Molecular Phylogenetics and Evolution. 54(1), 291-301.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G., and Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology. 25, 1965-1978.

Hijmans R.J., Guarino, L., Bussink, C., Mathur, P. Mariana, C., Barrentes, I., and Rojas, E. (2004). DIVA-GIS version 5.2 manual. Available, http://www.diva-gis.org/Materials.htm.

Hladik, C.M., Charles-Dominque, P., and Petter, J.-J. (1980). Feeding strategies of five nocturnal prosimians in the dry forest of the west coast of Madagascar. In Charles-Dominique, P., Cooper, H.M., Hladik, A. Hladik, C.M., Pagès, E., Pariente, G.F., Petter-Rousseaux, A., Petter, J.-J., and Schilling, A. (Eds.). *Nocturnal Malagasy Primates, Ecology, Physiology and Behaviour* (Pp. 41-73). New York: Academic Press.

Holdaway, R.J., and Sparrow, A.D. (2006). Assembly rules operating along a primary riverbed-grassland successional sequence. Journal of Ecology. 94, 1092-1102.

Holt, R.D. (1993). Ecology at the mesoscale, the influence of regional processes on local communities. In R. Ricklefs and D. Schluter (Eds.). *Species Diversity in Ecological Communities* (Pp. 77-88). Chicago: University of Chicago Press.

Holt, B.G., Lessard, J., Borregaard, M.K., Fritz, S.A., Araujo, M.B., Dimitrov, D., Fabre, P.-H., Graham, C.H., Graves, G.R., Jonsson, K.A., Nogues-Bravo, D., Wang, Z., Whittaker, R.J., Fjeldsa, J., and Rahbek, C. (2013). An update of Wallace's zoogeographic regions of the world. Science. 339(6115), 74-78.

Holyoak, M., Leibold, M.A., and Holt, R.D. (2005). *Metacommunities, Spatial Dynamics and Ecological Communities*. Chicago: University of Chicago Press.

Horsup, A., and Marsh, H. (1992). The diet of the Allied Rock-wallaby, *Petrogale assimilis*, in the Wet-Dry Tropics. Wildlife Research. 19, 17-33.

Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton: Princeton University Press.

Hubbell, S.P. (2005). Neutral theory in community ecology and the hypothesis of functional equivalence. Ecology. 19, 166-172.

Hubbell, S.P. (2006). Neutral theory and the evolution of ecological equivalence. Ecology. 87, 1387-1398.

Huston, M.A. (1999). Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. Oikos 86, 393 -401.

Hutchinson, G.E. (1957). Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology. 22, 415-427.

Ikin, K., Barton, P.S., Knight, E., Lindenmayer, D.B., Fischer, J., and Manning, A.D. (2014). Bird community responses to the edge between suburbs and reserves. Oecologia. 174(2), 545-557.

Irwin, M.T. (2009). Sadabe Activities. Sadabe.org, 24 Nov. 2009. Web. 01 Nov. 2014. <http://sadabe.org/activities.html>.

Irwin, M.T. , Junge, R.E., Raharison, J.L., and Samonds, K.E. (2010) Variation in physiological health of Diademed Sifakas across intact and fragmented forest at Tsinjoarivo, eastern Madagascar. American Journal of Primatology. 72, 1013-1025.

Irwin, M.T., Wright, P.C., Birkinshaw, C., Fisher, B.L., Gardner, C.J., Glos, J., Goodman, S.M., Loiselle, P., Rabeson, P., Raharison, J-L., Raherilalo, M.J., Rakotondravony, D., Raselimanana, A., Ratsimbazafy, J., Sparks, J.S., Wilmé, L., and Ganzhorn, J.U. (2010). Patterns of species change in anthropogenically disturbed forests of Madagascar. Biological Conservation. 143(10), 2351-2362.

IUCN (2014). The IUCN *Red List of Threatened Species.* Version 2014.3. <http://www.iucnredlist.org>. Downloaded on 1 February 2015.

IUCN, and UNEP. (2014). *The World Database on Protected Areas (WDPA*). UNEP-WCMC. Cambridge, UK. www.protectedplanet.net

Jablonski. D., and Sepkoski Jr., J.J. (1996). Paleobiology, community ecology, and scales of ecological pattern. Ecology. 77, 1367-1378.

Jaccard, P. (1901) Distribution de la flore alpine dans le bassin des Dranses et dans quelques régions voisines. Bulletin de la Société Vaudoise des Sciences Naturelles. 37, 241-272.

Jansa, S.A., Goodman, S.M., and Tucker, P.K. (1999). Molecular phylogeny and biogeography of the native rodents of Madagascar (Muridae, Nesomyinae), a test of the single-origin hypothesis. Cladistics. 15, 253-270.

Jenkins, P.D. (2003). *Microgale*, shrew tenrecs. In S.M. Goodman, and J.P. Benstead (Eds.). *The Natural History of Madagascar* (Pp. 1273-1278). Chicago: The University of Chicago Press.

Jenkins, P.D., Brescacin, C.R., Duxbury, C.V., Elliott, J.A., Evans, J.A., Grablow, K.R., Hillegass, M., LyonO, B.N., Metzger, G.A., Olandese, M.L. Pepe, D., Silvers, G. A., Suresch, H. N., Thompson, T. N., Trexler, C. M., Williams, G. E., Williams, N. C., Williams, S. E. (2007). Does size matter for dispersal distance? Global Ecology and Biogeography. 16(4), 415-425.

Jenkins, P.D., and Goodman, S.M. (1999). A new species of *Microgale* (Lipotyphla, Tenrecidae) from isolated forest in southwestern Madagascar. Bulletin of the Natural History Museum London (Zoology). 64,155-164.

Jenkins, P.D. (1993). A new species of *Microgale* (Insectivora, Tenrecidae) from eastern Madagascar with an unusual dentition. American Museum Novitates. 3067, 1-11.

Jepson, P., and Whittaker, R. J. (2002), Ecoregions in Context: a Critique with Special Reference to Indonesia. Conservation Biology, 16, 42-57.

Johnson, C. (2006). *Australia's Mammal Extinctions, a 50000 Year History*. Cambridge: Cambridge University Press.

Jolly, A. (1966). *Lemur Behaviour, a Madagascar Field Study*. Chicago: University of Chicago Press.

Jokat, W. Boebel, T., Konig, M., and Meyer, U. (2003). Timing and geometry of early Gondwana breakup. Journal of Geophysical Research. 108, 2428-2442.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J.C., Orme, D.L., Safi, K., Sechrest, W., Boakes, E.H., Carbone, C., Connolly, C., Cutts, M.J., Foster, J.K., Grenyer, R., Habib, M., Plaster, C.A., Price, S.A., Rigby, E.A., Rist, J., Teacher, A., Bininda-Emonds, O.R.P., Gittleman, J.L., Mace, G.M., Purvis, A., and Michener, W.K. (2009). PanTHERIA, a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology. 90, 2648.

Jones, M., Tuomisto, H., Borcard, D., Legendre, P., Clark, D., and Olivas, P. (2008). Explaining variation in tropical plant community composition, influence of environmental and spatial data quality. Oecologia. 155(3), 593-604.

Jones, M.M., Tuomisto, H., Clark, D.B., and Olivas, P. (2006). Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. Journal of Ecology. 94(1), 181-195.

Jürges, V., Kitzler, J., Zingg, R., and Radespiel, U. (2013). First insights into the social organisation of Goodman's mouse lemur (*Microcebus lehilahytsara*) -testing predictions from socio-ecological hypotheses in the Masoala hall of Zurich Zoo. Folia Primatoligica. 84(1), 32-48.

Jury, M.R. (2003). The climate of Madagascar. In S.M. Goodman, J.P. Benstead (Ed.), *The Natural History of Madagascar* (Pp. 76-87). Chicago: University of Chicago Press.

Kamilar, J.M. (2009). Environmental and geographic correlates of the taxonomic structure of primate communities. American Journal of Physical Anthropology. 139, 382-393.

Kamilar, J.M., and Beaudrot, L. (2013). Understanding primate communities, recent developments and future directions. Evolutionary Anthropology. 22(4), 174-185.

Kamilar, J.M., Beaudrot, L., and Reed, K. (2014). The influences of species richness and climate on the phylogenetic structure of African haplorhine and strepsirrhine primate communities. International Journal of Primatology. 35(6), 1105-1121.

Kamilar, J.M., and Cooper, N. (2013). Phylogenetic signal in primate behaviour, ecology and life history. Transactions of the Royal Society B. 368, 20120341

Kamilar J.M., and Guidi, L.M. (2010). The phylogenetic structure of primate communities, variation within and across continents. Journal of Biogeography. 37, 801-813.

Kamilar, J.M., Martin, S.K., Tosi, A.J. (2009). Combining biogeographic and phylogenetic data to examine primate speciation, an example using cercopithecin monkeys. Biotropica. 41, 514-519.

Kamilar, J.M., and Muldoon, K.M. (2010). The climatic niche diversity of Malagasy primates, a phylogenetic approach. PLOS ONE. 5, e11073. doi:10.1371/journal.pone.0011073.

Kamilar, J.M., and Ledogar, J.A. (2011). Species co-occurrence patterns and dietary resource competition in primates. American Journal of Physical Anthropology. 144, 131-139.

Kamilar, J.M., Muldoon, K.M., Lehman, S.M., and Herrera, J.P. (2012). Testing Bergmann's rule and the resource seasonality hypothesis in Malagasy primates using GIS-based climate data. American Journal of Physical Anthropology. 147, 401-408.

Kappeler, P.M. (2003). *Mirza coquereli*, Coquerel's dwarf lemur. In Goodman S.M., Benstead J.P. (Eds.). *The Natural History of Madagascar* (Pp. 1316-1318). Chicago: University of Chicago Press.

Kappeler, P.M., Rasoloarison, R.M., Razafimanantsoa, L., Walter, L., and Roos, C. (2005). Morphology, behaviour and molecular evolution of giant mouse lemurs (*Mirza* spp.). Gray, 1870, with description of a new species. Primate Report. 71, 3-26.

Karlson, R.H., and Hurd, L.E. (1993). Disturbance, coral reef communities, and changing ecological paradigms. Coral Reefs. 12, 117-125.

Karpanty, S.M. (2006). Direct and indirect impacts of raptor predation on lemurs in southeastern Madagascar. International Journal of Primatology. 27, 239-261.

Karst, J., Gilbert, B., and Lechowicz, M.J. (2005). Fern community assembly, the roles of chance and the environment at local and intermediate scales. Ecology. 86, 2473-2486.

Kay, E.H., and Hoekstra, H.E. (2008). Rodents. Current Biology. 18(10), R406-R410.

Keddy, P.A. (1992). Assembly and response rules, two goals for predictive community ecology. Journal of Vegetation Science. 3, 157-164.

Keil, P., Schweiger, O., Kühn, I., Kunin, W. E., Kuussaari, M., Settele, J., Storch, D. (2012). Patterns of beta diversity in Europe, the role of climate, land cover and distance across scales. Journal of Biogeography. 39(8), 1473-1486.

Kelt, D.A., Brown, J.H., Heske, E.J., Marquet, P.A., Morton, S.R., Reid, J.R.W., Rogovin, K.A., and Shenbrot, G. (1996). Community structure of desert small mammals: comparisons across four continents. Ecology. 77(3), 746-761.

Kelt, D.A., Taper, M.L., and Meserve, P.L. (1995). assessing the impact of competition on community assembly, a case study using small mammals. Ecology. 76(4), 1283-1296.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Webb, C.O. (2010). Picante, R tools for integrating phylogenies and ecology. Bioinformatics. 26(11), 1463-1464.

Kembel, S.W. (2009). Disentangling niche and neutral influences on community assembly, assessing the performance of community phylogenetic structure tests. Ecology Letters. 12, 949-960.

Kirk, E.C. (2004). Comparative morphology of the eye in primates. Anatomical Record. 281A(1), 1095-1103.

Kirk, E.C. (2006). Eye morphology in cathemeral lemurids and other mammals. Folia Primatologica. 77, 27-49; Erratum. (2007). Folia Primatologica.78, 69-72.

Kisel, Y., and Barraclough, T.G. (2010). Speciation has a spatial scale that depends on levels of gene flow. The American Naturalist. 175(3), 316-334.

Klein, J. (2002). Deforestation in the Madagascar Highlands - established `truth' and scientific uncertainty. GeoJournal. 56 (3), 191-199.

Kobbe, S., Ganzhorn, J.U., Dausmann, K.H. (2011). Extreme individual flexibility of heterothermy in free-ranging Malagasy mouse lemurs (*Microcebus griseorufus*). Journal of Comparative Physiology B. 181, 165-173

Kohn, D.D., and Walsh, D.M.. (1994). Plant species richness-the effect of island size and habitat diversity. Journal of Ecology. 82, 367-377.

Korhonen, J.J., Soininen, J., and Hillebrand, H. (2010). A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems. Ecology. 91, 508-517.

Kraft, N., and Ackerly, D. (2010). Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. Ecological Monographs. 80, 401-422.

Kraft, N., Ackerly, D., and Valencia, R. (2008). Functional traits and niche-based tree community assembly in an Amazonian forest. Science. 322, 580-582.

Kraft, N.J.B., Comita, L.S., Chase, J.M., Sanders, N.J., Swenson, N.G., Crist, T.O., Myers, J.A. (2011). Disentangling the drivers of β-diversity along latitudinal and elevational gradients. Science. 333(6050), 1755-1758.

Kraft, K., Cornwell, W., Webb, C., and Ackerly, D. (2007). Trait conservatism, community assembly, and the phylogenetic structure of ecological communities. The American Naturalist. 170, 271-283.

Kreft, H., and Jetz, W. (2013). Comment on "An Update of Wallace's Zoogeographic Regions of the World". Science. 341(6144), 343-343.

Laakkonen, J., Goodman, S.M., Duchemin, J-B., and Duplantier, J-M. (2003). Trypomastigotes and potential flea vectors of the endemic rodents and the introduced *Rattus rattus* in the rainforests of Madagascar. Biodiversity and Conservation. 12, 1775-1783.

LaFleur, M., Sauther, M., Cuozzo, F., Yamashita, N., Youssouf, I.A.J., and Bender, R. (2014). Cathemerality in wild ring-tailed lemurs (*Lemur catta*). in the spiny forest of Tsimanempetsotsa National Park, camer trap data and preliminary behavioral observations. Primates. 55, 207-217.

Lahann, P., Schmid, J., and Ganzhorn, J.U. (2006).Geographic variation in life history traits of *Microcebus murinus* in Madagascar. International Journal of Primatology 27, 983-999.

Laliberté, E. (2008). Analyzing or explaining beta diversity, comment. Ecology. 89, 3232-3237.

Laliberté, E., and Legendre, P (2010). A distance-based framework for measuring functional diversity from multiple traits. Ecology. 91(1)., 299-305.

Laliberté, E., Paquette, A., Legendre, P., and Bouchard, A. (2009). Assessing the scale-specific importance of niches and other spatial processes on beta diversity, a case study from a temperate forest. Oecologia. 159(2), 377-388.

Laliberté, E., and Shipley, B. (2011). FD, measuring functional diversity from multiple traits, and other tools for functional ecology. *R package version 1.0-11*.

Lamb, E., Mengersen, K., Stewart, K., and Attanayake, U. (2014). Spatially Explicit Structural Equation Modeling. Ecology. 95, 2434–2442.

Langrand, O., and Goodman, S.M. (1997). *Inventaire biologique forêt de Vohibasia et d'Isoky-Vohimena. Recherches pour le Développement, Série Sciences Biologiques No. 12*. Antananarivo: Centre d'Information et de Documentation Scientifique et Technique.

Lasky, J.R., and Keitt T.H. (2013). Reserve size and fragmentation alter community assembly, diversity and dynamics. The American Naturalist. 182, E142-E160.

Laughlin, D.C., Fulé, P.Z., Huffman, D.W., Crouse, J., and Laliberté, E. (2011). Climatic constraints on trait-based forest assembly. Journal of Ecology. 99, 1489-1499.

Lovegrove, B., and Génin, F. (2008). Torpor and hibernation in a basal placental mammal, the Lesser Hedgehog Tenrec *Echinops telfairi*. Journal of Comparative Physiology B. 178(6), 691-698.

Lavorel, S., and Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits, revisiting the Holy Grail. Functional Ecology. 16, 545-556.

Lawes, M.J., and Eeley, H.A.C. (2008). Are local patterns of anthropoid primate diversity related to patterns of diversity at a larger scale? Journal of Biogeography. 27, 1421-1435.

Lawton, J.H. (1983). Plant architecture and the diverstiy of phytophagous insects. Annual Review of Entomology. 28, 23-39.

Lawton, J.H., Lewinsohn, T.M., and Compton, S.G. (1993). Patterns of diversity for the insect herbivores on bracken. In Ricklefs R.E. and D. Schluter (Eds). *Species Diversity in Ecological Communities* (Pp. 178-184). Chicago: University of Chicago Press.

Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Bongers, F., and Poorter, L. (2014). Functional traits and environmental filtering drive community assembly in a species-rich tropical system. Ecology. 91(2), 386-398.

Lee, K.E., Ellis, W.A.H., Carrick, F.N., Corley, S.W., Johnston, S.D., Baverstock, P.R., Seddon, J.M. (2013). Anthropogenic changes to the landscape resulted in colonization of koalas in north-east New South Wales, Australia. Austral Ecology. 38(3), 355-363.

Lee, K.E., Seddon, J.M., Corley, S., Ellis, W.A.H., Johnston, S.D., de Villiers, D.L., Preece, H.J., and Carrick, F.N. (2010). Genetic variation and structuring in the threatened koala populations of Southeast Queensland. Conservation Genetics. 11, 2091-103.

Lees, D.C., Kremen, C., and Andriamampianina, L. (1999). A null model for species richness gradients, bounded range overlap of butterflies and other rainforest endemics in Madagascar. Biological Journal Linnean Society. 67, 529-584.

Legendre, P. (1993). Spatial autocorrelation, trouble of new paradigm? Ecology. 74(6), 1659-1673.

Legendre, P., Borcard, D., and Peres-Neto, P.R. (2005). Analyzing beta diversity, partitioning the spatial variation of community composition data. Ecological Monographs. 75(4), 435-450.

Legendre, P., Borcard, D., and Peres-Neto, P.R. (2008). Analyzing or explaining beta diversity, comment. Ecology. 89, 3238-3244.

Legendre, P., Dale, M.R.T., Fortin, M.J., Gurevitch, J., Hohn, M. and Myers, D. (2002). The consequences of spatial structure for design and analysis for ecological field surveys. Ecography. 25, 601-615.

Legendre, P., De Caceres, M., and Borcard, D. (2010). Community surveys through space and time, testing the space-time interaction in the absence of replication. Ecology. 91(1), 262-272.

Legendre, P., and Fortin, M.J. (1989). Spatial pattern and ecological analysis. Vegetation. 80, 107-138.

Legendre, P., and Gallagher, E. (2001). Ecologically meaningful transformations for ordination of species data. Oecologia, 129(2), 271-280.

Legendre, P., and Legendre, L. (1998). *Numerical Ecology 2nd Ed*. Amsterdam: Elsevier.

Legendre, P., and Legendre, L. (2012). *Numerical Ecology 3rd Ed*. Boston: Elsevier.

Lehman S.M. (2006). Nested distribution patterns and the histori-cal biogeography of the primates of Guyana. In Lehman S.M. and Fleagle J.G. (Eds.). *Primate Biogeography* (Pp. 63-80). New York: Springer.

Lehman, S.M. (2007). Ecological and phylogenetic correlates to body size in the Indriidae. International Journal of Primatology. 28(1), 183-210.

Lehman, S.M., Mayor, M., and Wright, P.C. (2005). Ecogeographic size variations in sifakas, a test of the resource seasonality and resource quality hypotheses. American Journal of Physical Anthropology. 126(3), 318-328.

Lehman, S.M., Nargolwalla, M., Faulkner, A., Taylor, A., and Lundy, R. (2007). A test of the optimal body size model for strepsirhines. International Journal of Primatology. 28(1), 211-230.

Lehner, B., and Doll, P. (2004). *Global Lakes and Wetlands Database, Lakes and Wetlands Grid (Level 3).* Washington, D.C.: World Wildlife Fund.

Lei, R., Engberg, S.E., Andriantompohavana, R., McGuire, S.M., Mittermeier, R.A., Zaonavrivelo, J.R., Brenneman, R.A., and Louis, E.E. (2008). Nocturnal lemur diversity at Masoala National Park. Special Publications of Museum of Texas Tech University. 53, 1-41.

Leibold, M.A., and McPeek, M.A. (2006). Coexistence of the niche and neutral perspectives in community ecology. Ecology. 87(6), 1399-1410.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., and Gonzalez, A. (2004). The metacommunity concept, a framework for multi-scale community ecology. Ecology Letters. 7(7), 601-613.

Lennon, J.J., Koleff, P., Greenwood, J.J.D., and Gaston KJ. (2001). The geographical structure of British bird distributions, diversity, spatial turnover and scale. Journal of Animal Ecology. 70, 966-979.

Levin, S.A. (1992). The problem of pattern and scale in ecology. Ecology. 73, 1943-1967.

Lichstein, J.W., Simons, T.R., and Franzreb, K.E. (2002). Landscape effects on breeding songbird abundance in managed forests. Ecological Applications. 12, 836-857.

Lindo, Z., and Winchester, N.N. (2007). Resident corticolous oribatid mites (Acari, Oribatida), decay in community similarity with vertical distance from the ground. Ecoscience. 14, 223-229.

Lindo, Z., and Winchester, N. (2009). Spatial and environmental factors contributing to patterns in arboreal and terrestrial oribatid mite diversity across spatial scales. Oecologia. 160(4), 817-825.

Lingoes, J.C. (1971). Some boundary conditions for a monotone analysis of symmetric matrices. Psychometrika. 36 (2), 195-203.

Liu, A., Folmer, H., and Oud, J.H.L. (2011). Estimating regression coefficients by W-based and latent variables spatial autoregressive models in the presence of spillovers from hotspots: evidence from Monte Carlo simulations. Letters in Spatial and Resource Sciences. 4, 71-80.

Lomolino, M.V. (2000). A species-based theory of insular zoogeography. Global Ecology and Biogeography. 9(1), 39-58.

Lomolino, M.V., and Davis, R. (1997). Biogeographic scale and biodiversity of mountain forest mammals of Western North America. Global Ecology and Biogeography Letters. 6(1), 57-76.

Londoño-Murcia, M.C., Tellez-Valdés, O., and Sánchez-Cordero, V. (2010). Environmental heterogeneity of World Wildlife Fund for Nature ecoregions and implications for conservation in Neotropical biodiversity hotspots. Environmental Conservation. 37(02), 116-127.

Loreau, M. (2000). Are communities saturated? On the relationship between α, β and γ diversity. Ecology Letters. 3, 73-76.

Loreau, M., and Mouquet, N. (1999). Immigration and the maintenance of local species diversity. American Naturalist. 154, 427-440.

Losos, J.B., Leal, M., Glor, R.E., de Queiroz, K., Hertz, P.E., Rodriguez Schettino, L., Larson, A. (2003). Niche lability in the evolution of a Caribbean lizard community. Nature. 424(6948), 542-545.

Losos, J.B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters. 11, 995-1007.

Louis, E.E., Coles, M.S., Andriantompohavana, R., Sommer, J.A., Engberg, S.E., Zaonarivelo, J.R., Mayor, M.I., and Brenneman, R.A. (2006). Revision of mouse lemurs (*Microcebus*) of eastern Madagascar. International Journal of Primatology. 27, 347-389.

Louis, E.E., Engberg, S.E., McGuire, S.M., McCormick, M.J., Randriamampionona, R., Ranaivoarisoa, J.F., Bailey, C.A., Mittermeier, R.A., and Lei, R. (2008). Revision of the mouse lemurs, *Microcebus* (Primates, Lemuriformes), of northern and northwestern Madagascar with descriptions of two new species at Montagne d'Ambre National Park and Antafondro Classified Forest. Primate Conservation. 23, 19-38.

Lowe, W.H., and McPeek, M.A. (2014). Is dispersal neutral? Trends in Ecology and Evolution. 29(8), 444-450.

MacArthur, R.H., and Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist. 101, 377-385.

MacArthur, R.H., and Wilson, E.O. (1963). An equilibrium theory of insular zoogeography. Evolution. 17(4), 373-387.

MacArthur, R.H., and Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton: Princeton University Press.

Mackey, B.G., and Lindenmayer, D.B. (2001). Towards a hierarchical framework for modelling the spatial distribution of animals. Journal of Biogeography. 28, 1147-1166.

Mac Nally, R., Fleishman, E., Bulluck, L.P., and Betrus, C.J. (2004). Comparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies, Journal of Biogeography. 31(6), 917-929.

Magurran, A.E., and McGill, B.J. (2010). *Biological Diversity, Frontiers in Measurement and Assessment*. Oxford: Oxford University Press.

Mahazotahy, S., Goodman, S.M., and Andriamanalina, A. (2006). Notes on the distribution and habitat preferences of *Galidictis grandidieri* Wozencraft, 1986 (Carnivore, Eupleridae), a poorly known endemic species of southwestern Madagascar. Mammalia. 70, 595-598.

Maminirina, C.P., Goodman, S.M., and Raxworthy, C.J. (2008). Les micro-mammifères (Mammalia, Rodentia, Afrosoricida et Soricomorpha) du massif du Tsaratanana et biogéographie des forêts de montagne de Madagascar. Zoosystema. 30, 695-721.

Marcstrom, V., Hoglund, N., and Krebs, C.J. (1990). Periodic fluctuations in small mammals at Boda, Sweden from 1961 to 1988. Journal of Animal Ecology. 59, 753-761.

Marshall, A.J., Cannon, C.H., and Leighton, M. (2009). Competition and niche overlap between gibbons (*Hylobates albibarbis*) and other frugivorous vertebrates in Gunung Palung National Park, West Kalimantan, Indonesia. In Lappan S., Whittaker D.J. (Eds.). *The Gibbons, New Perspectives on Small Ape Socioecology and Population Biology (*Pp. 161-188). Chicago: University of Chicago Press.

Martin, A.P. (2002). Phylogenetic approaches for describing and comparing the diversity of microbial communities. Applied and Environmental Microbiology. 68(8), 3673-3682.

Martin, R.D. (1972). Adaptive radiation and behaviour of the Malagasy lemurs. Philosophical Transactions of the Royal Society of London B Biological Science. 264, 295-352.

Martin, R.D. (1973). A review of the behaviour and ecology of the lesser mouse lemur (*Microcebus murinus* JF Miller 1977). In Michael, R. P., and Crook, J. H. (Eds). *Comparative Ecology and Behaviour of Primates* (Pp. 1-68). London: Academic Press.

Mason, N.W.H., de Bello, F., Mouillot, D., Pavoine, S., and Dray, S. (2013). A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. Journal of Vegetation Science. 24(5), 794-806.

Mason, N.W.H., Mouillot, D., Lee, W.G., and Wilson, J.B. (2005). Functional richness, functional evenness and functional divergence, the primary components of functional diversity. Oikos. 111, 112-118.

Mason, N., and Pavoine, S. (2013). Does trait conservatism guarantee that indicators of phylogenetic community structure will reveal niche-based assembly processes along stress gradients? Journal of Vegetation Science. 24, 820-833.

Maxwell, S., Burbidge, A.A., and Morris, K. (1996). *The 1996 Action Plan for Australian Marsupials and Monotremes.* Wanneroo, Australia: Wildlife Australia, Environment Australia. http://www.environment.gov.au/resource/action-plan-australian-marsupials-and-monotremes.

Mayfield, M.M., Boni, M.E., Daily, G.C., and Ackerly, D. (2005). Species and functional diversity of native and human-dominated plant communities. Ecology. 86, 2365-2372.

McCain, C.M. (2005). Elevational gradients in diversity of small mammals. Ecology. 86(2), 366-372.

McClain, C.R., Stegen, J.C., and Hurlbert, A.H. (2011). Dispersal, environmental niches and oceanic-scale turnover in deep-sea bivalves. Proceedings of the Royal Society B. 282(1805), 1-10.

McCoy, E.D., and Bell, S.S. (1991). Habitat structure: the evolution and diversification of a complex topic. In S.S. Bell, E.D. McCoy and H.R. Mushinsky (Eds.). *Habitat Structure: The Physicial Arrangement of Objects In Space* (Pp. 3-27). London: Chapman and Hall.

McGill, B.J. (2003). A test of the unified neutral theory of biodiversity. Nature. 422, 881-885.

McGill, B.J., Hadly, E.A., and Maurer, B.A. (2005). Community inertia of quaternary small mammal assemblages in North America. Proceedings of the National Academy of Sciences USA. 102, 16701-16706.

McGill, B.J., Enquist, B.J., Weiher, E., and Westoby, M. (2006). Rebuilding community ecology from functional traits. Trends in Ecology and Evolution. 21, 178-185.

McGill, B.J., Maurer, B.A., and Weiser, M.D. (2006). Empirical evaluation of neutral theory. Ecology. 87, 1411-1423.

McGraw, W.S., and Bshary, R. (2002). Association of terrestrial mangabeys (*Cercocebus atys*) with arboreal monkeys: experimental evidence for the effects of reduced ground predator pressure on habitat use. International Journal of Primatology. 23(2), 311-325.

McIntosh, R.P. (1967). An Index of Diversity and the Relation of Certain Concepts to Diversity. Ecology. 48, 392-404.

McLachlan-Troup, T.A., Dickman, C.R., and Grant, T.R. (2010). Diet and dietary selectivity of the platypus in relation to season, sex and macroinvertebrate assemblages. Journal of Zoology. 280, 237-246.

McNab, B.K. (2008). An analysis of the factors that influence the level and scaling of mammalian BMR. Comparative Biochemistry and Physiology Part A, Molecular and Integrative Physiology. 151(1), 5-28.

Meachen, J.A., and Roberts, T.E. (2014). A Novel Multiscale Assessment of Community Assembly across Time, Space, and Functional Niche. The American Naturalist. 183(5), 585-599.

Meier, B., and Albignac, R. (1989). Hairy-eared Dwarf Lemur rediscovered (*Allocebus trichotis*). Primate Conservation. 10, 30.

Meier, B., and Albignac, R. (1991). Rediscovery of *Allocebus trichotis* Guenther 1875 (Primates) in Northeast Madagascar. Folia Primatologica. 56, 57-63.

Meijaard, E., and Groves, C.P. (2006). The geography of mammals and rivers in mainland southeast Asia. In S.M. Lehman and J. Fleagle (Eds.). *Primate Biogeography*, *Progress and Prospects* (Pp. 305-329). New York: Springer.

Meldrum, D.J., Dagosto, M., and White, J. (1997). Hindlimb suspension and hind foot reversal in *Varecia variegata* and other arboreal mammals. American Journal of Physical Anthropology. 103, 85-102.

Mendoza, M., Goodwin, B., and Criado, C. (2004). Emergence of community structure in terrestrial mammal-dominated ecosystems. Journal of Theoretical Ecology. 230, 203-214.

Menna, J. (2003). *Predators with Pouches: the Biology of Carnivorous Marsupials*. Collingwood, Victoria: CSIRO.

Meynard, C.N., Devictor, V., Mouillot, D., Thuiller, W., Jiguet, F. and Mouquet, N. (2011). Beyond taxonomic diversity patterns, how do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? Global Ecology and Biogeography. 20, 893-903.

Miljutin, A., and Lehtonen, J.T. (2008). Probability of competition between introduced and native rodents in Madagascar: an estimation based on morphological traits. Estonian Journal of Ecology. 57(2), 133-152.

Miller, G.H., Fogel, M.L., Magee, J.W., Gagan, M.K., Clarke, S.J., and Johnson, B.J. (2005). Ecosystem collapse in Pleistocene Australia and a human role in megafaunal extinction. Science. 309, 287-290.

Mittermeier, R., Ganzhorn, J., Konstant, W., Glander, K., Tattersall, I., Groves, C., Rylands, A.B., Hapke, A., Ratsimbazafy, J., Mayor, M.I., Louis, E.E., Rumpler, Y., Schwitzer, C., and Rasoloarison, R.M. (2008). Lemur diversity in Madagascar. International Journal of Primatology. 29(6), 1607-1656.

Mittermeier, R., Louis, E.E.Jr., Richardson, M., Schwitzer, C., Langrand, O., Rylands, A.B., Hawkins, F, Rajaobelina, S., Ratsimbazafy, J., Rasoloarison, R. Roos, C., Kappeler, P.M., and J. Mackinnon (2010). *Lemurs of Madagascar 3rd Ed.* Arlington: Conservation International.

Mokany, K., and Roxburgh, S.H. (2010). The importance of spatial scale for trait-abundance relations. Oikos. 119(9), 1504-1514.

Morin, X., and Lechowicz, M.J. (2008). Contemporary perspectives on the niche that can improve models of species range shifts under climate change. Biology Letters. 4, 573-576.

Morland, H.S. (1993). Seasonal behavioral variation and its relationship to thermoregulation in ruffed lemurs (*Varecia variegata variegata*), In Kappeler, P.M., and J.U.Ganzhorn (Eds.). L*emur Social Systems and their Ecological Basis* (Pp.193-203). New York: Plenum Press.

Morlon, H., Schwilk, D.W., Bryant, J.A., Marquet, P.A., Rebelo, A.G., Tauss, C., Green, J.L. (2011). Spatial patterns of phylogenetic diversity. Ecology Letters. 14(2), 141-149.

Morris, D.W. (2005). On the roles of time, space and habitat in a boreal small mammal assemblage, predictably stochastic assembly. Oikos. 109(2), 223-238.

Mouchet, M.A., Villéger, S., Mason, N.W.H., and Mouillot, D. (2010). Functional diversity measures, an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology. 24(4), 867-876.

Mouillot, D., Villéger, S., Scherer-Lorenzen, M., and Mason, N.W.H. (2011). Functional Structure of Biological Communities Predicts Ecosystem Multifunctionality. PLOS ONE. 6(3), e17476.

Mouquet, N., Devictor, V., Meynard, C.N., Munoz, F., Bersier, L.-F., Chave, J., Thuiller, W. (2012). Ecophylogenetics, advances and perspectives. Biological Reviews. 87(4), 769-785.

Mueller, A.E., and Thalmann, U. (2002). The biology of the fat-tailed dwarf lemur (*Cheirogaleus medius* E. Geoffrey 1812), New results from the field. Evolutionary Anthropology. 11(S1), 79-82.

Muldoon, K.M., and Goodman, S.M. (2010). Ecological biogeography of Malagasy non-volant mammals, community structure is correlated with habitat. Journal of Biogeography. 37(6), 1144-1159.

Muldoon, K.M., Crowley, B.E., Godfrey, L.R., Rasoamiaramanana, A., Aronson, A., Jernvall, J., Wright, P.C., and Simons, E.L. (2012). Early Holocene fauna from a new subfossil site, a first assessment from Christmas River, south central Madagascar. Madagascar Conservation and Development. 7, 23-29.

Muldoon, K.M., and Simons, E.L. (2007). Ecogeographic size variation in small-bodied subfossil primates from Ankilitelo, SW Madagascar. American Journal of Physical Anthropology. 134, 152-161.

Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., and Thuiller, W. (2012). How to measure and test phylogenetic signal. Methods in Ecology and Evolution. 3, 743-756.

Mutschler, T., and Tan, C. (2003). *Hapalemur*, bamboo or gentle lemurs. In S.M. Goodman, J. Benstead (Eds.). *The Natural History of Madagascar* (Pp. 1324-1328). Chicago: University of Chicago Press.

Nekola, J.C., and White, P.S. (1999). The distance decay of similarity in biogeography and ecology. Journal of Biogeography. 26, 867-878.

Nicoll, M.E. (2003). *Tenrec eucaudatus*, Tenrec, *Tandraka, Tandraka*, In Goodman, S.M., and Benstead, J.P. (Eds.). *The Natural History of Madagascar* (Pp 1283-1287). Chicago: The University of Chicago.

Nijman, V., and Nekaris, K. (2010). Checkerboard patterns, interspecific competition, and extinction: lessons from distribution patterns of tarsiers (*Tarsius*) and slow lorises (*Nycticebus*) in insular Southeast Asia. International Journal of Primatology. 31(6), 1147-1160

Nowak, R.M. (1999). *Walker's Mammals of the World* (6th edition). Baltimore: Johns Hopkins University Press.

Nowak, R.M. (2005). *Walker's Marsupials of the World*. Baltimore: Johns Hopkins University Press.

NPWS (2002). Forrest's Mouse (*Leggadina forresti*) and Sandy Inland Mouse (*Pseudomys hermannsburgensis*) Recovery Plan. NSW National Parks and Wildlife Service, Hurstville NSW.

Nunn, C.L., and Barton, R.A. (2001). Comparative methods for studying primate adaptation and allometry. Evolutionary Anthropology. 10(3), 81-98.

Oates, J.F., Whitesides, G.H., Davies, A.G., Waterman, P.G., Green, S.M., Dasilva, G.L., and Mole, S. (1990). Determinants of variation in tropical forest primate biomass, new evidence from West Africa. Ecology.71, 328-343.

Okie, J.G.and Brown, J. H. (2009). Niches, body sizes, and the disassembly of mammal communities on the Sunda Shelf islands. Proceedings of the National Academy of Science. 106(2), 19679-19684.

Økland, R.H. (1999). On the variation explained by ordination and constrained ordination axes. Journal of Vegetation Science. 10, 131-136.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., and Wagner, H. (2013). vegan, Community Ecology Package. R package version 2.0-10. http://CRAN.R-project.org/package=vegan

Oksanen, L., and Oksanen, T. (1992). Long-term microtine dynamics in north Fennoscandian tundra, the vole cycle and lemming chaos. Ecography. 15, 226-236.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Henry, M., Stevens, L.L., and Wagner, H. (2008). Vegan, Community Ecology Package, R package version 1.13-1.

Oliveri, G., Zimmermann, E., Randrianambinina, B., Rasoloharijaona, S., Rakotondravony, D., Guschanski, K., and Radespiel, U. (2007). The ever-increasing diversity in mouse lemurs, three new species in north and northwestern Madagascar. Molecular Phylogenetics and Evolution. 43, 309-327.

Olson, D.M., and Dinerstein, E. (1998). The Global 200, A representation approach to conserving the earth's most biologically valuable ecoregions. Conservation Biology. 12(3), 502-515.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R. (2001). Terrestrial ecoregions of the world, a new map of life on Earth. Bioscience. 51(11), 933-9

Olson, D.M., and Goodman, S.M. (2003). Phylogeny and biogeography of tenrecs. In, Goodman, S.M., Benstead, J.P. (Eds.). *The Natural History of Madagascar* (Pp. 1235-1242). Chicago: University of Chicago Press.

Olson, L.E., Rakotomalala, Z., Hildebrandt, K.B.P., Lanier, H.C., Raxworthy, C.J., and Goodman, S.M. (2009). Phylogeography of *Microgale brevicaudata* (Tenrecidae) and description of a new species from western Madagascar. Journal of Mammalogy. 90, 1095-1110.

Ossi, K.M., and Kamilar, J.M. (2006). Environmental and phylogenetic correlates of *Eulemur* behavior and ecology (Primates, Lemuridae). Behavioral Ecology and Sociobiology. 61, 53-64.

Overdorff, D. (1993). Similarities, differences, and seasonal patterns in the diets of *Eulemur rubriventer* and *Eulemur fulvus rufus* in the Ranomafana National Park, Madagascar. International Journal of Primatology. 14, 721-753.

Overdorff, D. (1996). Ecological correlates to social structure in two lemur species in Madagascar. American Journal of Physical Anthropology. 100, 487-506.

Pacala, S.W., and Tilman, D. (1994). Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. American Naturalist. 143, 222-257.

Palmer, M.W. (1991). Patterns of species richness among North Carolina hardwood forests: tests of two hypotheses. Journal of Vegetation Science. 2, 361-366.

Palmer M.W., and White, P.S. (1994). Scale dependence and the species-area relationship. American Naturalilst. 144, 717-740.

Pakeman, R.J. (2011). Functional diversity indices reveal the impacts of land use intensification on plant community assembly. Journal of Ecology. 99(5), 1143-1151.

Pakeman, R.J. (2014). Functional trait metrics are sensitive to the completeness of the species' trait data. Methods In Ecology And Evolution. 5(1), 9-15.

Paradis, E., Claude, J., and Strimmer, K. (2004). APE, Analyses of phylogenetics and evolution in R language. Bioinformatics. 20(2), 289-290.

Parga, J.A. (2011). Nocturnal ranging by a diurnal primate, are ring-tailed lemurs (*Lemur catta*) cathemeral? Primates. 52(3), 201-205.

Pastorini, J., Martin, R.D., Ehresmann, P., Zimmerman, E., and Forstner, M.R. (2001). Molecular phylogeny of the lemur family Cheirogaleidae (Primates) based on mitochondrial DNA sequences. Molecular Phylogenetics and Evolution. 19, 45-56.

Pastorini, J., Thalmann, U., and Martin, R.D. (2003). A molecular approach to comparative phylogeography of extant Malagasy lemurs. Proceedings of the National Academy of Sciences USA. 100, 5879-5884.

Pavoine, S., Baguette, M., and Bonsall, M.B. (2010) Decomposition of trait diversity among the nodes of a phylogenetic tree. Ecological Monographs. 80, 485-507.

Pavoine S., and Bonsall, M.B. (2011). Measuring biodiversity to explain community assembly, a unified approach. Biological Reviews. 86, 792-812.

Pavoine, S., Gasc, A., Bonsall, M.B., and Mason, N.W.H. (2013) Correlations between phylogenetic and functional diversity: mathematical artefacts or true ecological and evolutionary processes? Journal of Vegetation Science. 24, 781-793.

Pearson, D.L., and Juliano, S.A. (1993). Evidence for the influence of historical processes in co-occurrence and diversity of tiger beetles. In Ricklefs R.E., and Schluter, D. (Eds.). *Species Diversity in Ecological Communities. Historical and Geographical Perspectives* (Pp. 194-202). Chicago: University of Chicago Press.

Pearson, R.G., and Raxworthy, C.J. (2009). The evolution of local endemism in Madagascar, watershed versus climatic gradient hypotheses evaluated by null biogeographic models. Evolution. 63, 959-967.

Peres, C.A., and Janson, C.H. (1999). Species coexistence, distribution, and environmental determinants of neotropical primate richness: A community-level zoogeographic analysis. In Fleagle, J. G., Janson, C. H., and Reed, K. (Eds.). *Primate Communities* (Pp. 55-74). Cambridge: Cambridge University Press.

Peres-Neto, P.R., Legendre, P., Dray, S., and Borcard, D. (2006). Variation partitioning of species data matrices, estimation and comparison of fractions. Ecology. 87(10), 2614-2625.

Pestell, A.J.L., and Petit, S. (2007). Diet of the western pygmy possum, *Cercartetus concinuus* Gould (Marsupialia: Burramyidae), at Innes National Park, South Australia, and evalution of diet sampling methods. Australian Journal of Zoology. 55, 275-284.

Petchey, O.L., and Gaston, K.J. (2006). Functional diversity, back to basics and looking forward. Ecology Letters. 9, 741-758.

Peterson, D.L., and Parker, V.T. (1998). *Ecological Scale: Theory and Applications.* New York: Columbia University Press.

Petter, J.J. (1962). Ecological and behavioral studies of Madagascar lemurs in the field. Annals of the New York Academy of Sciences. 102, 267-281.

Pineda-Munoz, S., and Alroy, J. (2014). Dietary characterization of terrestrial mammals. Proceedings of The Royal Society B: Biological Sciences, 281(1789), 20141173-20141173.

Poizat, G., and Pont, D. (1996). Multi-scale approach to species-habitat relationships: juvenile fish in large river section. Freshwater Biology. 36, 611-622.

Potter, S., Eldridge, M.D.B., Taggart, D.A., and Cooper, S.J.B. (2012). Multiple biogeographic barriers identified across the monsoon tropics of northern Australia: phylogeographic analysis of the *brachyotis* group of rock-wallabies. Molecular Ecology. 21, 2254-2269.

Potts, M.D., Ashton, P.S., Kaufman, L.S., and Plotkin, J.B. (2002). Habitat patterns in tropical rain forests, a comparison of 105 plots in Northwest Borneo. Ecology. 83(10), 2782-2797.

Powzyk, J.A. (1997). *The socio-ecology of two sympatric indriids, Propithecus diadema diadema and Indri indri, a comparison of feeding strategies and their possible repercussions on species-specific behaviours.* PhD dissertation, Duke University. Durham, North Carolina.

Pozo-Montuy, G., Serio-Silva, J.C., and Bonilla-Sanchez, Y.M. (2011). Influence of the landscape matrix on the abundance of arboreal primates in fragmented landscapes. Primates. 52(2), 139-147.

Prinzing, A., Durka, W., Klotz, S., and Brandl, R. (2001). The niche of higher plants: evidence for phylogenetic conservatism. Proceedings of the Royal Society London B. 268(1483), 2383-2389.

Prugh, L.R., Hodges, K.E., Sinclair, A.R.E., and Brashares, J.S. (2008). Effect of habitat area and isolation on fragmented animal populations. Proceedings of the National Academy of Sciences. 105(52), 20770-20775.

Purschke, O., Schmid, B.C., Sykes, M.T., Poschlod, P., Michalski, S.G., Durka, W., Kühn, I., Winter, M., and Prentice, H.C. (2013), Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. Journal of Ecology. 101(4), 857-866.

Purvis, A., Cardillo, M., Grenyer, R., and Collen, B. (2005). Correlates of extinction risk: phylogeny, biology, threat and scale. In Purvis A, Gittleman J.L, Brooks T (Eds.). *Phylogeny and Conservation* (Pp. 295-316). Cambridge, UK: Cambridge University Press.

Qian, H., and Ricklefs, R.E (2007). A latitudinal gradient in large-scale beta diversity for vascular plants in North America. Ecology Letters. 10(8), 737-744.

Qian, H., and Ricklefs, R.E. (2012). Disentangling the effects of geographic distance and environmental dissimilarity on global patterns of species turnover. Global Ecology and Biogeography. 21, 341-351.

Qian, H., Ricklefs, R.E., and White, P.S. (2005). Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. Ecology Letters. 8, 15-22.

R Core Team (2014). R, A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Rabeantoandro, Z. (1997) *Contribution à l'étude biologique et écologique de Mungotictis decemlineata decemlineata (Grandidier, 1869) dans la forêt de Kirindy à Morondava*. Mémoire pour l'obtention de D.E.A., Université d'Antananarivo. Antananarivo, Madagascar.

Radespiel, U., Olivieri, G., Rasolofoson, D.W., Rakotondratsimba, G., Rakotonirainy, O., Rasoloharijaona, S., Randrianambinina, B., Ratsimbazafy, J., Ratelolahy, F., Randriamboavonjy, T., Rasolofoharivelo, T., Craul, M., Rakotozafy, L., and Randrianarison, R.M. (2008). Exceptional diversity of mouse lemurs (*Microcebus* spp.) in the Makira region with the description of one new species. American Journal of Primatology. 70, 1033-1046.

Radespiel, U., Reimann, W., Rahelinirina, M., and Zimmermann, E. (2006). Feeding ecology of sympatric mouse lemur species in northwestern Madagascar. International Journal of Primatology. 27, 311-321.

Rahel, F.J., Lyons, J.D., and Cochran, P.A. (1984). Stochastic or deterministic regulations of assemblage structure? It may depend on how the assemblage is defined. American Naturalist. 124, 583-589.

Raia, P. (2010). Phylogenetic community assembly over time in Eurasian Plio-Pleistocene mammals. Palaios. 25(5), 327-338.

Rakotondraparany, F., and Medard, J. (2005). *A rapid biological assessment of the Mantadia-Zahamena corridor, Madagascar, Bulletin RAP d'evaluation rapide 32.* Washington, D.C.: Conservation International.

Rakotondravony, D., Goodman, S.M., and Goodman, S.M. (1998). *Inventaire biologique Forêt d'Andranomay, Anjozorobe. Recherches pour le Développement, Série Sciences Biologiques No. 13*. Antananarivo: Centre d'Information et de Documentation Scientifique et Technique.

Rakotondravony, D., Randrianjafy, V., and Goodman, S.M. (2002). *Evaluation rapide de la diversité biologique des micromammifères de la Réserve Naturelle Intégrale d'Ankarafantsika.* Washington, D.C.: Conservation International.

Ralainasolo, F.B., Ratsimbazafy J.H., and Stevens N.J. (2008). Behavior and diet of the critically endangered *Eulemur cinereiceps* in the Manombo forest, southeast Madagascar. Madagascar Conservation and Development. 3(1), 38-43.

Ralison, J.M. (2008). Les lémuriens des forêts sèches malgaches. Malagasy Nature. 1, 135-156.

Ramaromilanto, B., Lei, R., Engberg, S.E., Johnson, S.E., Sitzmann, B.D., and Louis, E.E. (2009). Sportive lemur diversity at Mananara-Nord Biosphere Reserve, Madagascar. Occasional Papers, Museum of Texas Tech University. 286, 1-23.

Ramp, D., Wilson, V.K., and Croft, D.B. (2006). Assessing the impacts of roads in peri-urban reserves: Road-based fatalities and road usage by wildlife in the Royal National Park, New South Wales, Australia. Biological Conservation, 129(3), 348-359.

Randrianambinina, B., Rakotondravony, D., Radespiel, U., and Zimmerman, E. (2003). Seasonal changes in general activity, body mass and reproduction of two small nocturnal primates, a comparison of the golden brown mouse lemur (*Microcebus ravelobensis*) in Northwestern Madagascar and the brown mouse lemur (*Microcebus rufus*) in Eastern Madagascar. Primates. 44, 321-31.

Randrianarisoa, M., Rasamison, A., and Rakotozafy, L. (2001). Notes sur la faune lémurienne dans la Réserve Spéciale d'Ambohijanahary. Lemur News. 6, 5.

Randriatahina, G.H., and Rabarivola, J.C. (2004). Inventaire des lémuriens dans la partie nord-ouest de Madagascar et distribution d'*Eulemur macaco flavifrons*. Lemur News. 9, 7-9.

Rao, C.R. (1982). Diversity and dissimilarity coefficients: a unified approach. Theoretical Population Biology. 21, 24-43.

Raselimanana, A.P., and Goodman, S.M. (2004). *Inventaire floristique et faunistique de la forêt de Mikea, paysage écologique et diversité biologique d'une préoccupation majeure pour la conservation. Recherches pour le Développement, Série Sciences Biologiques No. 21*. Antananarivo: Centre d'Information et de Documentation Scientifique et Technique.

Rasoloarison, R.M., Goodman, S.M., and Ganzhorn, J.U. (2000). Taxonomic revision of mouse lemurs (*Microcebus*) in the western portions of Madagascar. International Journal of Primatology. 21, 963-1019.

Rasolonandrasana, B.P.N., and Goodman, S.M. (2006). The influence of fire on mountain sclerophyllous forests and their small-mammal communities in Madagascar. In E. M. Spehn, M. Liberman, and C. Körner (Eds.). *Land Use Change and Mountain Biodiversity* (Pp. 77-87). Boca Raton: Taylor and Francis.

Ratsirarson, J., and Goodman, S.M. (2000). *Monographie de la Forêt d'Ambohitantely. Recherches pour le Développement, Série Sciences Biologiques No. 16.* Antananarivo: Centre d'Information et de Documentation Scientifique et Technique.

Ravosa, M.J., Meyers, D.M., and Glander, K.E. (1993). Relative growth of the limbs and trunk in sifakas: heterochronic, ecological, and functional considerations. American Journal of Physical Anthropology. 92, 499–520.

Rawlins, D.R., and Handasyde, K.A. (2002). The feeding ecology of the striped possum *Dactylopsila trivirgata* (Marsupialia: Petauridae) in far north Queensland, Australia. Journal of Zoology. 257(2), 195-206.

Raxworthy, C.J., Andreone, F., Nussbaum, R.A., Rabibisoa, N., and Randriamahazo, H.R. (1998). Amphibians and reptiles of the Anjanaharibe-Sud Massif, Madagascar: Elevational distribution and regional endemicity. In A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud: with reference to elevational variation. Fieldiana. 90, 79-92.

Raxworthy, C.J., and Nussbaum, R.A. (1996). Montane amphibian and reptile communities in Madagascar. Conservation Biology. 10, 750-756.

Raxworthy, C.J., and Rakotondraparany, F. (1988). Mammals Report. Manongarivo Special Reserve, Madagascar 1987/88 Expedition Report (ed. by N. Quansah)., Pp. 121-131. Madagascar Environmental Research Group.

Razafimanantsoa, L. (2003). *Mungotictis decemlineata*, Narrow-striped Mongoose, Boky-boky. In Goodman, S.M., Benstead, J.P. (Eds.). *The Natural History of Madagascar* (Pp. 1357-1360). Chicago: University of Chicago Press.

Razafindratsima, O.H., Mehtani, S., and Dunham, A.E. (2013). Extinctions, traits and phylogenetic community structure, insights from primate assemblages in Madagascar. Ecography. 36(1), 47-56.

Read, D.G., and Fox, B.J. (1991). Assessing the habitat of the parma wallaby, *Macropus parma* (Marsupialia: Macropodidae). Wildlife Research. 18(4), 469-477.

Reed, K.E. (2008). Paleoecological patterns at the Hadar hominin site, Afar Regional State, Ethiopia. Journal of Human Evolution. 54, 743-768.

Reed, K.E., and Bidner, L.R (2004). Primate communities, Past, present, and possible future. American Journal of Physical Anthropology. 125(S39), 2-39.

Reed, K.E., and Fleagle, F.G. (1995). Geographic and climatic control of primate diversity. Proceedings of the National Academy of Sciences, USA. 92, 7874-7876.

Reeves, C., and De Wit, M. (2000). Making ends meet in Gondwana: retracing the transforms of the Indian Ocean and reconnecting continental shear zones. Terra Nova. 12(6), 272-280.

Remis, M. (1995). Effects of body size and social context on the arboreal activities of lowland gorillas in the Central African Republic. American Journal of Physical Anthropology. 97(4), 413-433.

Reynolds, H.L., Mittelbach, G.G., Darcy-Hall, T.L., Houseman, G.R., and Gross, K.L. (2007). No effect of varying soil resource heterogeneity on plant species richness in a low fertility grassland. Journal of Ecology. 95, 723-733.

Richard, A.F., and Dewar, R.E. (1991). Lemur ecology. Annual Review of Ecology, Evolution, and Sytematics. 22, 145-175.

Rickart, E.A. (2001). Elevational diversity gradients, biogeography, and the structure of montane mammal communities in the intermountain region of North America. Global Ecology and Biogeography. 10, 77-100.

Ricklefs, R.E. (1987). Community diversity, relative roles of local and regional processes. Science. 235(4785), 167-171.

Ricklefs, R.E. (2007). History and diversity: explorations at the intersection of ecology and evolution. The American Naturalist. 170(S2), S56-S70.

Ricklefs, R.E., and Schluter, D. (1993). *Species Diversity in Ecological Communities, Historical and Geographical Perspectives.* Chicago: University of Chicago Press.

Riddle, B.R. (2006). Conservation Biogeography. Journal of Biogeography 33, 2025-2026.

Ripley, S. (1967). The leaping of langurs: a problem in the study of locomotor adaptation. American Journal of Physical Anthropology. 26, 149-170.

Ritchie, E.G., Martin, J.K., Krockenberger, A.K., Garnett, S., and Johnson, C.N. (2008). Large-herbivore distribution and abundance: intra- and interspecific niche variation in the tropics. Ecological Monographs. 78(1), 105-122.

Roberts, R.G., Flannery, T.F., Ayliffe, L.K., Yoshida, H., Olley, J.M., Prideaux, G.J., Laslett, G.M., Baynes, A., Smith, M.A., Jones, R., and Smith, B.L. (2001). New Ages for the Last Australian Megafauna: Continent-Wide Extinction About 46,000 Years Ago. Science. 292(5523), 1888-1892.

Roberts, R.G., Jones, R., Spooner, N.A., Head, M.J., Murray, A.S., and Smith, M.A. (1994). The human colonisation of Australia: optical dates of 53,000 and 60,000 years bracket human arrival at Deaf Adder Gorge, Northern Territory. Quaternary Science Reviews. 13(5-7), 575-583.

Robinson, W., Brawn, J., and Robinson, S. (2000). Forest bird community structure in central Panama: influence of spatial scale and biogeography. Ecological Monographs. 70(2), 209-235.

Rojas, A.D., Körtner, G., and Geiser, F (2014). Torpor in free-ranging antechinus, does it increase fitness Naturwissenschaften. 101(2), 105-114.

Roll, U., Dayan, T., and Kronfeld-Schor, N. (2006). On the role of phylogeny in determining activity patterns of rodents. Evolutionary Ecology. 20(5), 479-490.

Rominger, A.J., Miller, T.E.X., and Collins, S.L. (2009). Relative contributions of neutral and niche-based processes to the structure of a desert grassland grasshopper community. Oecologia. 161(4), 791-800.

Ron, S.R. (2000). Biogeographic area relationships of lowland Neotropical rainforest based on raw distributions of vertebrate groups. Biological Journal of the Linnean Society. 71, 379-402.

Rosenzweig, M.L. (1995). *Species Diversity In Space And Time*. Cambridge: Cambridge University Press.

Ruf, T., Bieber, C., Arnold, W., and Millesi, E. (2012). Living in a seasonal world, thermoregulatory and metabolic adaptations. New York: Springer.

Ryan, J.M. (2003). *Nesomys*, Red Forest Rat, *Voalavo* Mena. In Goodman, S. M and Benstead, J.P. (Eds). *The Natural History of Madagascar*, Pp. 1388-1389. The University of Chicago Press, Chicago.

Ryan, J.M., Creighton, G.K., and Emmons, L.H. (1993). Activity patterns of two species of *Nesomys* (Muridae, Nesomyinae) in a Madagascar rainforest. Journal of Tropical Ecology, 9*,* 101-107.

Safi, K., Cianciaruso, M. V., Loyola, R.D., Brito, D., Armour-Marshall, K., and Diniz-Filho, J.A.F (2011). Understanding global patterns of mammalian functional and phylogenetic diversity. Philosophical Transactions of the Royal Society B, Biological Sciences. 366(1577), 2536-2544.

Salton, J.A., and Sargis, E.J. (2008). Evolutionary morphology of the Tenrecoidea (Mammalia) forelimb skeleton. In E.J. Sargis, and M. Dagosto (Eds.). *Mammalian Evolutionary Morphology* (Pp 51-71). Dordrecht: Springer Netherlands.

Salton, J.A., and Szalay, F.S. (2004). The tarsal complex of Afro-Malagasy Tenrecoidea, a search for phylogenetically meaningful characters. Journal of Mammalian Evolution. 11(2), 73-104.

Santos-Filho, M., Peres, C.A., da Silva, D.J., Sanaiotti, T.M. (2012). Habitat patch and matrix effects on small-mammal persistence in Amazonian forest fragments. Biodiversity and Conservation. 21(4), 1127-1147.

Sattler, T., Borcard, D., Arlettaz, R., and Bontadina, F. (2010). Spider, bee, and bird communities in cities are shaped by environmental control and high stochasticity. Ecology. 91(11), 3343-3353.

Scarff, F.R., Rhind, S.G., and Bradley, J.S. (1998). Diet and foraging behaviour of brush-tailed phascogales (*Phascogale tapoatafa*) in the jarrah forest of south-western Australia. Wildlife Research. 25, 511-526.

Scheckenbach, F., Hausmann, K., Wylezich, C., Weitere, M., and Arndt, H. (2010). Large-scale patterns in biodiversity of microbial eukaryotes from the abyssal sea floor. Proceedings of the National Academy of Science USA. 107, 115-120.

Schleuter, D., Daufresne, M., and Massol, F. (2010). A user's guide to functional diversity indices. Ecological Monographs. 80(3), 469-484.

Schluter, D. (2000). Ecological character displacement in adaptive radiation. The American Naturalist. 156, S4-S16.

Schmid, J. (1999). Sex-specific differences in activity patterns and fattening in the gray mouse lemur (*Microcebus murinus*) in Madagascar. Journal of Mammalogy. 80(3), 749-757.

Schmid, J. (2000). Daily torpor in the gray mouse lemur (*Microcebus murinus*) in Madagascar, energetic consequences and biological significance. Oecologia. 123, 175-183.

Schmid, J., Ruf, T., and Heldmaier, G. (2000). Metabolism and temperature regulation during daily torpor in the smallest primate, the pygmy mouse lemur (*Microcebus myoxinus*) in Madagascar. Journal of Comparative Physiology B. 170(1), 59-68.

Schmid, J., and Alonso, L.E. (2005). *A rapid biological assessment of the Mantadia-Zahamena Corridor, Madagascar. Bulletin RAP d'evaluation rapide, No.32.* Washington, D.C.: Conservation International.

Schmid, J., and Smolker, R. (1998). Lemurs of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar. A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar, with reference to elevational variation. Fieldiana. 90, 227-238.

Schmid, J. (2000). Daily torpor in the gray mouse lemur (*Microcebus murinus*) in Madagascar, energetic consequences and biological significance. Oecologia. 123, 175-183.

Schmid, J., Fietz, J., and Rakotobe, Z.L.R. (2005). *Lemurs of the Mantadia-Zahamena corridor. A rapid biological assessment of the Mantadia-Zahamena corridor, Madagascar. Bulletin RAP d'evaluation rapide 32.* Washington, D.C.: Conservation International.

Schmidt, M. (2010). Locomotion and postural behavior. Advances in Science and Research. 5, 23-39.

Scholz, F., and Kappeler, P.M. (2004). Effects of water scarcity on the ranging behavior of *Eulemur fulvus rufus*. International Journal of Primatology. 25, 599-613.

Schrama, M., Berg, M.P., Olff, H. (2012). Ecosystem assembly rules: the interplay of green and brown webs during salt marsh succession. Ecology. 93, 2353-2364.

Schreier, B.M., Harcourt, A.H., Coppeto, S.A., and Somi, M.F. (2009). Interspecific competition and niche separation in primates, a global analysis. Biotropica. 41, 283-291.

Schülke, O., and Ostner, J. (2007). Physiological ecology of cheirogaleid primates, variation in hibernation and torpor. Acta Ethologica. 10(1), 13-21.

Schwitzer, C., Glatt, L., Nekaris, K.A.I., and Ganzhorn, J.U. (2011). Responses of animals to habitat alteration, an overview focussing on primates. Endangered Species Research. 14(1), 31-38.

Shi, J.J., Chan, L.M., Rakotomalala, Z., Heilman, A. M., Goodman, S.M., and Yoder, A.D. (2013). Latitude drives diversification in Madagascar's endemic dry forest rodent *Eliurus myoxinus* (subfamily Nesomyinae). Biological Journal of the Linnean Society. 110, 500-517.

Shipley, B. (2002). *Cause and Correlation in Biology. A User's Guide to Path Analysis, Structural Equations and Causal Inference*. Cambridge: Cambridge University Press.

Shipley, B. (2010). Community assembly, natural selection and maximum entropy models. Oikos. 119(4), 604-609.

Shipley, B., Laughlin, D.C., Sonnier, G., and Otfinowski, R. (2011). A strong test of a maximum entropy model of trait-based community assembly. Ecology. 92, 507-517.

Shipley, B. Vile, D., and Garnier, E. (2006). From plant traits to plant communities: a statistical mechanistic approach to biodiversity. Science. 314(5800), 812-814.

Shulman, M.J., Ogden, J.C., Ebersole, J.P., McFarland, W.N., Miller, S.L., and Wolf, N.G. (1983). Priority effects in the recruitment of juvenile coral reef fishes. Ecology. 64, 1508-1513.

Siefert, A., Ravenscroft, C., Weiser, M.D., Weiser, and Swenson, N.G. (2013) Functional beta-diversity patterns reveal deterministic community assembly processes in eastern North American trees. Global Ecology and Biogeography. 22(6), 682-691.

Silvertown, J., McConway, K.J., Gowing, D.J., Dodd, M.E., Fay, M.F., Joseph, J.A., and Dolphin, K. (2006). Absence of phylogenetic signal in the niche structure of meadow plant communities. Proceedings of the Royal Society of London B. 273, 39-44.

Simmen, B., Tamaud, L., and Hladik, A. (2012). Leaf nutritional quality as a predictor of primate biomass, further evidence of an ecological anomaly within prosimian communities in Madagascar. Journal Tropical Ecology. 28,141-151.

Simmen, B., Hladik, A., and Ramasiarisoa, P. (2003). Food intake and dietary overlap in native Lemur catta and Propithecus verreauxi and introduced Eulemur fulvus at Berenty, southern Madagascar. International Journal of Primatology. 24, 948-967.

Simons, E.L., Burney, D.A., Chatrath, P.S.; Godfrey, L.R., Jungers, W.L., Rakotosamimanana, B. (1995). AMS 14C Dates for Extinct Lemurs from Caves in the Ankarana Massif, Northern Madagascar. Quaternary Research. 43(2), 249-254

Simpson, G.G. (1953). *Evolution and Geography, an Essay on Historical Biogeography with Special Reference To Mammals*. Eugene, Oregon: State System of Higher Education.

Simpson, G.G. (1964). Species density of North American recent mammals. Systematic Zoology. 13(2), 57-73.

Smith, A., and Ganzhorn, J. (1996). Convergence in community structure and dietary adaptation in Australian possums and gliders and Malagasy lemurs. Australian Journal of Ecology. 21, 31-46.

Smith T.W., and Lundholm J.T. (2010). Variation partitioning as a tool to distinguish between niche and neutral processes. Ecography. 33, 648-655

Smith, R.J., and Jungers, W.L. (1997). Body mass in comparative primatology. Journal of Human Evolution 32, 523-599.

Soarimalala, V., and Goodman, S.M. (2008). New distributional records of the recently described and endangered shrew tenrec *Microgale nasoloi* (Tenrecidae, Afrosoricida) from central western Madagascar. Mammalian Biology 73, 468-471.

Soarimalala, V. (2008). Les petits mammifères non-volants des forêts sèches malgaches. Malagasy Nature. 1, 106-134.

Soininen, J., McDonald, R., and Hillebrand, H. (2007). The distance decay of similarity in ecological communities. Ecography. 30(1), 3-12.

Sokol, E.R., Benfield, E.F., Belden, L.K., and Valett, H.M. (2011). The assembly of ecological communities inferred from taxonomic and functional composition. The American Naturalist. 177(5), 630-644.

Sommer, S. (2003). *Hypogeomys antimena*, Malagasy Giat Jumping Rat, Vositse, Votsotsa. In S.M. Goodman and J.P. Benstead (Eds.). *The Natural History of Madagascar* (Pp. 1383-1385). Chicago: The University of Chicago Press.

Sorg, J., Ganzhorn, J., and Kappeler, P. (2003). Forestry and research in the Kirindy Forest / Centre de Formation Professionnelle Forestière. In Goodman S.M. and Benstead, J. (Eds.). *The Natural History of Madagascar* (Pp. 1512-1519). Chicago: University of Chicago Press.

Sorg J.P., Rohner U. (1996). Climate and tree phenology of the dry deciduous forest of the Kirindy Forest. Primate Report. 46, 57-80.

Spasojevic, M.J., and Suding, K.N. (2012). Inferring community assembly mechanisms from functional diversity patterns, the importance of multiple assembly processes. Journal of Ecology. 100(3), 652-661.

Sprent, J.A., and McArthur, C. (2002). Diet and diet selection of two species int eh macropodid browser-grazer continuum: do they eat what they 'should'? Australian Journal of Zoology. 50, 183-192.

Stefano, J., and Newell, G.R. (2008). Diet selection by the Swamp Wallaby (*Wallabia bicolor*): feeding strategies under conditions of changed food availability. Journal of Mammology. 89(6), 1540-1549.

Stegen, J.C., and Hurlbert, A.H. (2011). Inferring Ecological Processes from Taxonomic, Phylogenetic and Functional Trait β-Diversity. PLOS ONE. 6(6), e20906.

Stephenson, P.J. (2003a). *Hemicentetes*, streaked tenrec. In S.M. Goodman, and J.P. Benstead (Eds.). *The Natural History of Madagascar* (Pp. 1281-1283). Chicago: The University of Chicago Press.

Stephenson, P.J. (2003b). Liptotyphla (ex Insectivora), *Geogale aurita*, Large-eared Tenrec. In S.M. Goodman, and J.P. Benstead (Eds.). *The Natural History of Madagascar* (Pp. 1281-1283). Chicago: The University of Chicago Press.

Stephenson, P.J. (1991). *Reproductive energetics of the Tenrecidae (Mammalian, Insectivora)*. PhD dissertation, University of Aberdeen. United Kingdom: ProQuest/UMI. (Publication No. DX97817.)

Stephenson, P.J. (1993). The small mammal fauna of Réserve Spéciale d'Analamazaotra, Madagascar, the effects of human disturbance on endemic species diversity. Biodiversity and Conservation. 2, 603-615.

Stephenson, P.J. (1994a). Notes on the biology of the fossorial tenrec, *Oryzorictes hova* (Insectivora, Tenrecidae). Mammalia. 58, 312-315.

Stephenson, P.J. (1994b). Resting metabolic rate and body temperature in the aquatic tenrec, *Limnogale mergulus* (Insectivora, Tenrecidae). Acta Theriologica. 39, 89-92.

Stephenson, P.J., Randriamahazo, H.J.A.R., Rakotoarison, N., and Racey, P.A. (1994). Conservation of mammalian species diversity in Ambohitantely Special Reserve, Madagascar. Biological Conservation. 69, 213-218.

Sterling, E.J., and McFadden, K. (2000). Rapid census of lemur populations in the Parc National de Marojejy, Madagascar. A floral and faunal inventory of the Parc National de Marojejy, Madagascar, with reference to elevational variation. Fieldiana. 97, 265-278.

Stevens, N.J., and O'Connor, P.M. (2006). Abiotic and biotic factors as predictors of species richness on Madagascar. In S.M. Lehman and J.G. Fleagle (Eds.). *Primate Biogeography* (Pp. 269-300). New York: Springer.

Stevens, R.D., Cox, S.B., Strauss, R.E., and Willig, M.R. (2003). Patterns of functional diversity across an extensive environmental gradient, vertebrate consumers, hidden treatments and latitudinal trends. Ecology Letters. 6(12), 1099-1108.

Stevens, R.D., Gavilanez, M.M, Tello, J.S., and Ray, D.A. (2012). Phylogenetic structure illuminates mechanistic effect of environmental heterogeneity on community organization. Journal of Animal Ecology. 81, 455-462.

Stevenson, P.R. (2001). The relationship between fruit production and primate abundance in Neotropical communities. Biological Journal of the Linnean Society. 72(1), 161-178.

Stirrat, S.C. (2002). Foraging ecology of the agile wallaby (*Macropus agilis*) in the wet-dry tropics. Wildlfe Research. 29, 347-361.

Stirrat, S.C. (2004). Activity budgets of the agile wallaby, *Macropus agilis*. Australian Journal of Zoology. 52, 49-64.

Stokes, C.J., and Archer, S.R. (2010). Niche differentiation and neutral theory: an integrated perspective on shrub assemblages in a parkland savanna. Ecology. 91, 1152-1162.

Stubbs, W.J., and Wilson, J.B. (2004). Evidence for limiting similarity in a sand dune community. Journal of Ecology. 92(4), 557-567.

Su, D., and Harrison, T. (2008). Ecological implications of the relative rarity of fossil hominins at Laetoli. Journal of Human Evolution. 55, 672–681.

Sussman, R. (1974). Ecological distinctions in overlapping Lemur species. In, Martin R, Doyle G, and Walker A. (Eds.). *Prosimian Biology* (Pp. 75-108). London: Duckworth Publishing.

Sutherland, J.P. (1974). Multiple stable points in natural communities. American Naturalist. 108(964), 859-873.

Swenson, N.G. (2011). The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity. American Journal of Botany. 98(3), 472-480.

Swenson, N.G., and Enquist, B. (2009). Opposing assembly mechanisms in a Neotropical dry forest, implications for phylogenetic and functional community ecology. Ecology. 90(8), 2161-2170.

Swenson, N., Enquist, B., Pither, J., and Thompson, J. (2006). The problem and promise of scale dependency in community phylogenetics. Ecology. 87(10), 2418-2424.

Svenning, J., Fløjgaard, C., Marske, K. A., Nógues-Bravo, D., Norm, S., and Normand, S. (2011). Applications of species distribution modeling to paleobiology. Quaternary Science Reviews. 30(21-22), 2930-2947.

Svenning, J.-C., Kenner, D.A., Stallard, R.F., Engelbrecht, B.M.J., and Wright, S.J. (2004). Ecological determinism in plant community structure across a tropical forest landscape. Ecology. 85(9), 2526-2538.

Szalay, F.S. (1994). *Evolutionary History of the Marsupials and an Analysis of Osteological Characters*. New York: Cambridge University Press.

Tan, C.L. (1999). Group composition, home range size, and diet of three sympatric bamboo lemur species (Genus *Hapalemur*) in Ranomafana national Park, Madagascar. International Journal of Primatology. 20(4), 547-566.

Tan, J., Ryberg, W.A., and Jiang, L. (2012). Species phylogenetic relatedness, priority effects, and ecosystem functioning. Ecology. 93, 1164-1172.

Tattersall, I. (1982). *The Primates of Madagascar.* New York: Columbia University Press.

Tattersall, I. (1987). Cathemeral activity in primates, a definition. Folia Primatologica. 49, 200-202.

Tattersall, I. (2007). Madagascar's Lemurs, Cryptic diversity or taxonomic inflation Evolutionary Anthropology, Issues, News, And Reviews. 16(1)., 12-23.

ter Braak, C.J.F., and Prentice, C.I. (1988). A theory of gradient analysis. Advances in Ecological Research. 18, 271-317.

Telfer, W.R., and Bowman, D.M.J.S. (2006). Diet of four rock-dwelling macropods in the Australian monsoon tropics. Austral Ecology. 31, 817-827.

Thalmann, U., and Geissmann, T. (2005). New species of woolly lemur *Avahi* (Primates, Lemuriformes) in Bemaraha (Central Western Madagascar). American Journal of Primatology. 67, 371-376.

Thomas, H., Kidney, D., Rubio, P., and Fanning, E. (2005). *The southern Mikea, a biodiversity survey.* United Kingdom: Society for Environmental Exploration.

Thompson, R., and Townsend, C. (2006). A truce with neutral theory, local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. Journal of Animal Ecology. 75(2), 476-484.

Thalmann, U. (2000). Lemur diversity and distribution in western Madagascar - inferences and predictions using a cladistics approach. In Lourenco, W.R., and Goodman, S.M. (Eds.), *Diversité et Endemise à Madagascar* (Pp. 191-202). Paris: Mémoires de la Société de Biogéographie.

Thuiller, W., Gallien, L., Boulangeat, I., de Bello, F., Munkemuller, T., Roquet, C., and Lavergne, S. (2010). Resolving Darwin's naturalization conundrum: a quest for evidence. Diversity and Distributions. 16, 461-75

Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton: Princeton University Press.

Tilman, D., and Pacala, S. (1993). The maintenance of species richness in plant communities. In R.E. Ricklefs and D. Schluter (Ed.), *Species Diversity in*

Ecological Communities, Historical and Geographical Perspectives (Pp. 13-25). Chicago: University of Chicago Press.

Tokeshi, M. (1999). *Species Coexistence, Ecological and Evolutionary Perspectives.* Oxford: Blackwell Science.

Tuomisto, H. (2010a). A diversity of beta diversities, straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography. 33, 2-22.

Tuomisto, H. (2010b). A diversity of beta diversities, straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. Ecography. 33, 23-45.

Tuomisto, H. (2010c). A consistent terminology for quantifying species diversity? Yes, it does exist. Oecologia. 164, 853-860.

Tuomisto, H., and Ruokolainen, K. (2006). Analyzing or explaining beta diversity? Understanding the targets of different methods of analysis. Ecology. 87(11), 2697-2708.

Tuomisto, H., Ruokolainen, K., and Yli-Halla, M. (2003). Dispersal, environment, and floristic variation of Western Amazonian forests. Science. 299(5604)., 241-244.

Turbill, C., Bieber, C., Ruf, T. (2011). Hibernation is associated with increased survival and the evolution of slow life histories among mammals. Proceedings of the Royal Society, B, London. 278, 3355-3363.

Turner, J. (2004). *Mammals of Australia: an Introduction to Their Classification, Biology and Distribution*. Sofia: Pensoft.

Turney, C.S.M., Bird M.I., Fifield L.K., Roberts R.G., Smith M., Dortch C.E., Grün R., Lawson E., Ayliffe L.K., Miller G.H., Dortch J., and Cresswell R.G. (2001). Early human occupation at Devil's Lair, southwestern Australia 50,000 years ago. Quaternary Research. 55(1), 3-13.

Van der Putten, W.H., Macel, M., and Visser, M.E. (2010). Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philosophical Transcations B. 365(1549), 2025-2034.

Van Dyck, S., and Strahan, R. (2006). *The Mammals of Australia, 3rd Edition*. Sydney, New South Wales, Australia: Reed New Holland.

Vasey, N. (2000). Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*, I. Interspecific patterns. American Journal of Physical Anthropology. 112, 411-431.

Vasey, N. (2002). Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*, II. Intraspecific patterns. American Journal of Physical Anthropology, 118, 169-183.

Vences, M., Wollenberg, K.C., Vieites, D.R., and Lees, D.C. (2009). Madagascar as a model region of species diversification. Trends in Ecology and Evolution. 24(8), 456-465.

Vignieri, S.N. (2005). Streams over mountains: influence of riparian connectivity on gene flow in the Pacific jumping mouse (*Zapus trinotatus*). Molecular Ecology. 14(7), 1925-1937.

Viguer, B. (2004). Functional adaptations in the craniofacial morphology of Malagasy primates: Shape variations associated with gumnivory in the family Cheirogaleidae. Annals of Anatomy-Anotomischer Anzeiger. 186, 495-501.

Villéger, S., Mason, N.W.H., and Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology. 89, 2290-2301.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V., and Messier, J. (2012). The return of variance: intraspecific variability in community ecology. Trends in Ecology and Evolution. 27(4), 244-252.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., and Garnier, E. (2007). Let the concept of trait be functional! Oikos. 116, 882-892.

Volkov, I., Banavar, J., Hubbell, S., and Maritan, A (2003). Neutral theory and relative species abundance in ecology. Nature. 424, 1035-1037.

Vololomboahangy, R., and Goodman, S. (IUCN SSC Afrotheria Specialist Group - Tenrec Section) (2008). *Setifer setosus*. The IUCN Red List of Threatened Species. Version 2014.3. <www.iucnredlist.org>.

Wade, T.G., Schultz, B.W., Wickham, J.D., and Bradford, D.F. (1998). Modeling the potential spatial distribution of beef cattle grazing using a Geographic Information System. Journal of Arid Environments. 38(2), 325-334.

Wahungu, G.M., Catterall, C.P., and Olsen, M.F. (1999). Selective herbivory by red-necked pademelon *Thylogale thetis* at rainforest margins: factors affecting predation rates. Austral Ecology. 24(6), 577-586.

Warnecke, L. Withers, P.C., Schleucher, E., and Maloney, S.K. (2007). Body temperature variation of free-ranging and captive souther brown bandicoots *Isoodon obesulus* (Marsupialia: Peramelidae). Journal of Thermal Biology. 32, 72-77.

Warren, R.D., and Crompton, R.H. (1998). Locomotor ecology of *Lepilemur edwardsi* and *Avahi occidentalis*. American Journal of Physical Anthropology. 104(4), 471-486.

Warren, D.L., Cardillo, M., Roasauer, D.F, and Bolnick, D.I. (2014). Mistaking geography for biology: inferring processes from speices distributions. Trends in Ecology and Evolution. 29(10), 572-580.

Watkins, A.J., and Wilson, J.B. (2003). Local texture convergence, a new approach to seeking assembly rules. Oikos. 102(3), 525-532.

Watts, C.H.S., and Aslin, H.J. (1981*). The Rodents of Australia*. Sydney: Angus and Robertson.

Webb, C.O. (2000). Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. American Naturalist. 156, 145-55.

Webb, C., Ackerly, D., and McPeek, M. (2002). Phylogenies and community ecology. Annual Review of Ecology. 33, 475-505.

Weigelt, A., Schumacher, J., Roscher, C., and Schmid, B. (2008). Does biodiversity increase spatial stability in plant communitybiomass? Ecology Letters. 11, 338-347.

Weiher, E., Clarke, G., and Keddy, P. (1998). Community assembly rules, morphological dispersion, and the coexistence of plant species. Oikos. 81, 309-322.

Weiher, E., and Keddy, P. (1995). Assembly rules, null models, and trait dispersion, new questions from old patterns. Oikos. 74(1), 159-164.

Weiher, E., and Keddy, P. (1999). Relative Abundance and Evenness Patterns along Diversity and Biomass Gradients. Oikos. 87(2), 355-361.

Weiher, E., and Keddy, P. (2001). Ecological Assembly Rules: Perspectives, Advances, Retreats. Cambridge, UK: Cambridge University Press.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., and Bentivenga, S. (2011). Advances, challenges and a developing synthesis of ecological community assembly theory. Philosophical Transactions of the Royal Society B: Biological Sciences. 366(1576), 2403-2413.

Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E., and Eriksoon, O. (1999). Challenging Theophrastus: A common core list of plant traits for functional ecology. Journal of Vegetation Science. 10, 609-620.

Wein, J. (2010). *Effects of ambient temperature on tropical hibernation in the lesser hedgehog tenrec, Echinops telfairi*. PhD dissertation, Universität Hamburg. Hamburg.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., and Wright, I.J. (2002). Plant ecological strategies: some leading dimensions of variation between species. Annual Review of Ecology, Evolution, and Systematics. 33, 125-159

Weyeneth, N., Goodman, S.M., and Ruedi, M. (2011). Do diversification models of Madagascar's biota explain the population structure of the endemic bat Myotis goudoti (Chiroptera, Vespertilionidae). Journal of Biogeography. 38(1), 44-54.

Whitehurst, A.S., Sexton, J.O., and Dollar, L. (2009). Land cover change in western Madagascar's dry deciduous forests: A comparison of forest changes in and around Kirindy Mite National Park. Oryx. 43, 275-283.

Whittaker, R.H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs. 30, 279-338.

Whittaker, R.H. (1972). Evolution and measurement of species diversity. Taxon. 21, 213-251.

Whittaker, R.J. (1998). *Island Biogeography*: *Ecology*, *Evolution* and. *Conservation*. Oxford University Press, Oxford.

Whittaker, R.J. (2006) Island species-energy theory. Journal of Biogeography. 33, 11-12.

Whittaker, R.J., Willis, K.J., and Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. Journal of Biogeography. 28, 453-470.

Wiens, J.A. (1989). Spatial scaling in ecology. *Functional Ecology, 3*(4), 385-397.

Wiens, J.J. (2011). The niche, biogeography and species interactions. Philosophical Transactions of the Royal Society B, Biological Sciences, 366(1576), 2336-2350.

Wiens, J.J., and Donoghue, M.J. (2004). Historical biogeography, ecology and species richness. Trends in Ecology and Evolution. 19(12), 639-644.

Wiens, J., and Graham, C. (2005). Niche conservatism, integrating evolution, ecology, and conservation biology. Annual Review of Ecology. 26, 519-539.

Williams, P., Gibbons, D., Margules, C.R., Rebelo, A., Humphries, C., and Pressey, R. (1996). A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. Conservation Biology. 10, 155-174.

Williams, S., Marsh, H., and Winter, J. (2002). Spatial scale, species diversity, and habitat structure, small mammals in Australian tropical rain forest. Ecology. 83(5), 1317-1329.

Willis, K.J., and Whittaker, R.J. (2002). Species diversity - scale matters. Science. 295, 1245-1248.

Wilmé, L., and Callmander, M.W. (2006). Les populations relique de primates: les Propitheques. Lemur News. 11, 24-31.

Wilmé, L., Goodman, S.M., and Ganzhorn, J.U. (2006). Biogeographic evolution of Madagascar's microendemic biota. Science. 312, 1063-1065.

Wilmé, L., Ravokatra, m., Dolch, R., Schuurman, D., Mathieu, E., Scheutz, H., and Waeber, P.O. (2012). Toponyms for centers of endemism in Madagascar. Madagascar Conservation and Development. 7(1), 30-40.

Wilson, D.E., and Mittermeier, R.A. (2009) *Handbook of the Mammals of the World, Volume 1 (Carnivores)*. Barcelona: Lynx Edicions.

Wilson, D.E., and Reeder, D.M. (2005). *Mammal Species of the World, 3rd Edition.* Baltimore: Johns Hopkins University Press.

Wilson, J.B., and Whittaker, R.J. (1995) Assembly rules demonstrated in a saltmarsh community. Journal of Ecology. 83, 801-807.

Wright, P.C. (1999). Lemur traits and Madagascar ecology, coping with an island environment. American Journal of Physical Anthropology. 110(S29), 31-72.

Wright, P.C., and Martin, L.B. (1995). Predation, pollination and torpor in two nocturnal primates, *Cheirogaleus major* and *Microcebus rufus* in the rain forest of Madagascar. In Alterman, L., Doyle, G., and Izard, K. (Eds.). *Creatures of the Dark, the Nocturnal Prosimians* (Pp. 45-60). New York: Plenum Press.

Wright, P.C., and Martin, L.B. (1995). Predation, pollination and tropor in two nocturnal prosimians, *Cheirogaleus major* and *Microcebus rufus* in the rain forest of Madagascar. In Alterman, L., Doyle, G.A., and Izard (Eds.). *Creatures of the Dark, the Nocturnal Prosimians* (Pp. 45-60). New York: M.K. Plenum Press.

Wright, P.C., Johnson, S.E., Irwin, M.T., Jacobs, R., Schlichting, P., Lehman, S., Louis, E.E., Arrigo-Nelson, S.J., Raharison, J.-L., Rafalirarison, R.R., Razafindratsita, V., Ratsimbazafy, J., Ratelolahy, F.J., Dolch, R., and Tan, C. (2008). The crisis of the critically endangered Greater Bamboo lemur (*Prolemur simus*). Primate Conservation. 23(1), 5-17.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Villar, R. (2004). The worldwide leaf economics spectrum. Nature. 428(6985), 821-827.

Wright, S. (1943). Isolation by distance. Genetics. 28(2), 114-138.

Woinarski, J.C.Z., Milne, D.J., and Wanganeen, G. (2001). Changes in mammal populations in relatively intact landscapes of Kakadu National Park, Australia. Austral Ecology. 26, 360-370.

Wood, D.H. (1971). The ecology of *Rattus fuscipes* and *Melomys cervinipes* (Rodentia: Muridaae) in a south-east Queensland rain forest. Australian Journal of Zoology. 19, 371-392.

Woodburne, M.O., and Case, J.A. (1996). Dispersal, vicariance, and the Late Cretaceous to Early Tertiary land mammal biogeography from South America to Australia. Journal of Mammalian Evolution. 3, 121-161.

Wootton, J.T. (2005). Field-parameterization and experimental test of the neutral theory of biodiversity. Nature. 433, 309-312.

World Conservation Monitoring Centre (1990). *Programme on Man and the Biosphre (MAB) Biosphere Reserves, Compilation 5, October 1990*. Cambridge, UK: IUCN Publications Services Unit.

Yamashita, N. (2002). Diets of two lemur species in different microhabitats in Beza Mahafaly special reserve, Madagascar. International Journal of Primatology. 23, 1025-1051.

Yoder, A.D., Cartmill, M. Ruvolo, M., Smith, K., and Vilgalys, R. (1996). Ancient single origin for Malagasy primates. Proceedings of the National Academy of Sciences. 93, 5122-5126.

Yoder, A.D., Burns, M.M., and Genin, F. (2002). Molecular evidence of reproductive isolation in sympatric sibling species of mouse lemurs. International Journal of Primatology. 23, 1335-1343.

Yoder, A.D., Burns, M.M., Zehr, S., Delefosse, T., Veron, G., Goodman S.M., and Flynn, J.J. (2003). Single origin of Malagasy Carnivora from an African ancestor. Nature. 421, 734-737.

Yoder, A.D., and Yang, Z. (2004). Divergence dates for Malagasy lemurs estimated from multiple gene loci: geological and evolutionary context. Molecular Ecology. 13(4), 757-773.

Youssouf, J.I.A., and Rasoazanabary, E. (2008). Discovery of *Macrotarsomys bastardi* at Beza Mahafaly Special Reserve, southwest Madagascar, with observations on the dynamics of small mammal interactions. Madagascar Conservation and Development. 3, 31-37.

Zilio, T., and Condit, R. (2007). The impact of neutrality, niche differentiation and species input on diversity and abundance distributions. Oikos. 116, 931-940.

Zobel, M. (1997). The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence. Trends in Ecology and Evolution. 12, 266-269.